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NUMBERS, REPRODUCTION AND GROWTH OF *CLETHRIONOMYS RUTILUS* (MAMMALIA: CRICETIDAE) FROM ISLANDS IN THE UPPER MACKENZIE RIVER AND ADJACENT MAINLAND

by

© DAWN MAUREEN DICKINSON

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL, 1976

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Numbers, reproduction and growth of *Clethrionomys rutilus* (Mammalia: Cricetidae) from islands in the upper Mackenzie River and adjacent mainland" submitted by Dawn Maureen Dickinson in partial fulfilment of the requirements for the degree of Master of Science.

W. D. Fuller
Supervisor

Date 18th October 1976

ABSTRACT

Populations of *Clethrionomys rutilus* were studied on seven islands in the upper Mackenzie River and at two sites on adjacent mainland by means of snap-trapping and autopsies of specimens thus obtained. Populations varied between islands and mainland sites, but were not negatively correlated with island size. All islands had higher populations of *C.rutilus* than mainland sites in August, and in five of seven islands the difference was significant.

Mean lengths and weights of reproductive young of the year females and overwintered females differed significantly. However, reproductive young females could not be distinguished individually from overwintered females in late July and August on the basis of length or weight, except at extremes of ranges. Mean lengths and weights of reproductive young of the year males and overwintered males also differed significantly and young reproductive males could clearly be distinguished individually from overwintered males on the basis of weight in late July and August. However, data obtained from tooth growth indicated that early-born males were virtually absent from all populations in late July and August.

Growth of the second upper molar (M^2) of young of the year in relation to sex,reproductive status,body length and weight showed that: a) M^2 crown length increased from time of weaning until closure of the anterior groove; b) environmental changes of season from June through August did not affect expression of M^2 growth in immatures of the same sex; c) there was a significant intersexual difference in M^2 length at the time of closure of the anterior groove and subsequent differences in rates of attrition of occlusal surface; d) there was no evidence of

cessation of M^2 growth by the last half of August, although growth of the axial skeleton of reproductive young (and most immatures) had ceased by that time; e) there was no evidence that pregnancy had any effect on M^2 growth, and f) young matured at an earlier stage of M^2 development in late June and July than in August.

Young were assigned to three seasonal age classes according to time of trapping and M^2 growth. These were early summer, mid summer and late summer. All early summer young matured except two males, and only one late summer young matured. There was no evidence to support a theory of inhibition of maturation of mid summer young by overwintered animals, nor by overwintered animals and mature early summer young, in spite of widely differing population indices. Evidence of wounding was slight and did not support a theory of inhibition through fighting.

Time of commencement of breeding differed substantially in at least two island populations, with the earlier breeding population achieving higher numbers in August than the population in which overwintered females were primiparous in mid June. Data supported a theory of a threshold of sensitivity to decreasing daylength primarily determining maturation of young of the year, rather than a theory of social inhibition, although the latter is not necessarily excluded.

Some information was obtained on other cricetids, principally *Peromyscus maniculatus*.

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In early spring, H.Hurtak enthusiastically live-trapped and cared for voles at Heart Lake Zoological Station,N.W.T. for an experiment that was planned to test sensitivity to decreasing daylength in juvenile *Clethrionomys gapperi*, held in large outside pens. However, the majority of the voles and/or their offspring declined to stay and participate. During the summer, assistance in the field was provided at various times by A. Shostak, R. Heimbecker, D. Hollingdale, T. Herman, G. Dyke, M. Fuller and G. Fuller.

Dr.B. Chernik made some helpful suggestions regarding statistical analysis. Dr. A. Martell suggested an additional method of analysis and discussed comparative methods of aging embryos. P. Pearlstone patiently instructed me in the ritual that is proper to a program and a computer.

I wish to thank Dr.J.O.Murie for reading and discussing the manuscript with me while he was still on sabbatical leave, and also Dr. G.E. Ball for his critical review of the manuscript at short notice. I am grateful to Dr.W.A. Fuller for his active help during field work and for his advice, criticism and encouragement during all phases of the research project.

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INTRODUCTION

The size and structure of late summer populations of a promiscuous or polygamous, polyestrous and relatively short-lived small rodent, with a discrete breeding season, are dependent in large measure on the extent of summer dispersal and the number of young of the year that mature and reproduce within the breeding season of their birth. The following study was undertaken to investigate some aspects of these two components of the population dynamics of the northern red-backed vole *Clethrionomys rutilus*.

Krebs *et al.* (1969) found that populations of two *Microtus* spp. that were fenced within 0.8 ha grassland plots, which were open to natural predators, achieved, and for a time maintained, densities much higher than those of control populations before declining. The results of that study led MacArthur (1972) to speculate on the relationship of dispersal to the size of an area in which a population is enclosed. In the sense that all animal populations are enclosed in islands, MacArthur suggested that high densities associated with enclosures, which he termed the Kreb's effect, would only occur on islands within a certain range of size. Accordingly the first hypothesis tested in the following study was that in late summer the relative numbers of *C. rutilus* and/or all cricetids on islands of grossly similar habitat and within the same region would be negatively correlated with island size - mainland being considered the largest island.

Sadleir (1969) reviewed much of the literature dealing with evidence for involvement of social factors in inhibiting maturation of several species of microtines. Koshkina's study (1965) of *C. rutilus* in the taiga of the Salair foothills, U.S.S.R. (54°00' N, 85°00' E) was

given as an example of high numbers of overwintered animals inhibiting maturation and reproduction of young of the year. In Kilpisjärvi, Finnish Lapland (69°00' N, 49°00' E), Kalela (1957) compared reproduction and densities of populations of *C. rufocanus* over three years and concluded that the fecundity rate of juvenile voles was density dependent - males having a lower threshold than females.

Schwarz *et al.* (1964) cited observations made by numerous Russian workers that in many species of small rodents, individuals born in spring mature and reproduce within the calendar year of their birth, whereas those born later in the season do not mature. Similar observations have been made in the case of *C. glareolus* in England (Brambell and Rowlands 1936); *C. gapperi* and *C. rutilus* in the Northwest Territories (Fuller 1969); *C. rufocanus* in Finland (Kalela 1957) and *Microtus arvalis* in France (Martinet 1967) and Germany (Reichstein 1964). Schwarz *et al.* (1964) showed experimentally that, while temperature and food may have had some effect, daylength was the critical factor in determining chronological age at maturation of *Lagurus lagurus*. Reichstein (1964) concluded from experiments that daylength, temperature, and food affected chronological age at maturation of *M. arvalis*. Accordingly, the second hypothesis that was tested in this study was that regardless of overwintered population densities, animals that are weaned in June or early in July would attain maturity, those weaned after July would not attain maturity and that maturation of those weaned in the interim period would be negatively correlated with the numbers of mature animals.

The major species for testing the hypotheses was the microtine rodent *C. rutilus*. In the course of the study small numbers of two other microtines, *Microtus pennsylvanicus* and *Phenacomys intermedius*, and moderate numbers of the cricetine *Peromyscus maniculatus* were obtained. When Cricetidae is mentioned in the text, tables or figures it refers to all four species. The only other small mammals obtained were insectivores belonging to the family Soricidae.

STUDY AREA

Location

The study was carried out during the summer of 1973 in the vicinity of Fort Providence, Northwest Territories (61°20'N, 117°40'W). Day (1968) described geology, soils and climatic conditions for this area.

Two mainland sites and seven islands of various sizes were chosen on the basis of 1) accessibility and 2) plant communities where white spruce (*Picea glauca*) was dominant. The two larger islands are named on the National Topographic Series (1:250,000) as Providence and Green Islands. The remaining five were named for the purpose of the study, with lamentable lack of imagination, as Islands 1, 2, 3, Round and Long (Figure 1). The two mainland sites were named after their nearest access points - Old Ferry Road and Simpson Junction. Relative sizes of islands and distances from nearest colonizing sources are shown in Tables 1 and 2.

While white spruce was the dominant tree, aspen poplar (*Populus tremuloides*), balsam poplar (*P. balsamifera*) and white birch (*Betula papyrifera*) were also components of the forest canopy. The shrub layer included willow (*Salix* spp.), alder (*Alnus* spp.) *Shepherdia canadensis*, *Rosa* spp. and *Arctostaphylos uva-ursa*. Ground cover consisted of various species of mosses, lichens, grasses, sedges and herbs, together with fallen logs and litter. Low, sloping shores subject to spring flooding were characterised by species of willow and pioneer riparian vegetation. They were not included in estimates of island size and were not trapped. While variation in vegetation both within and between sites was noted it

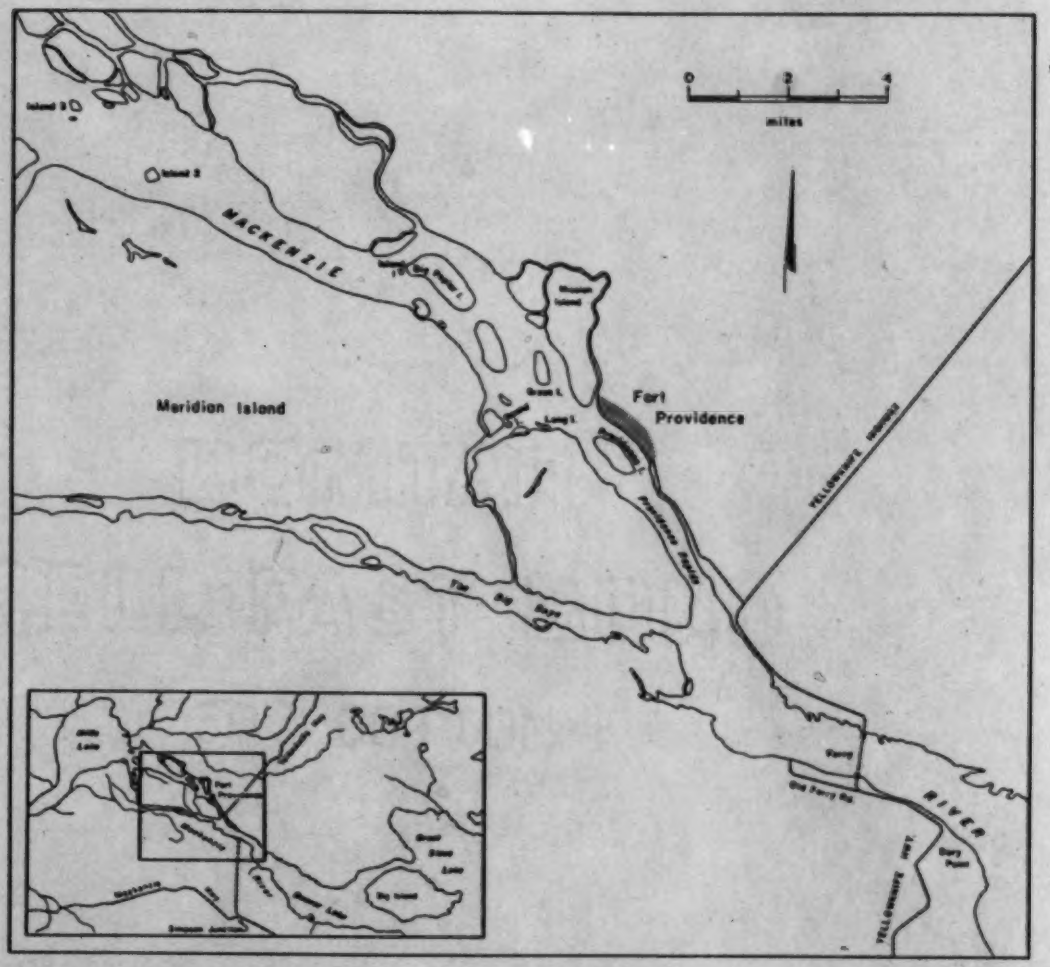


Figure 1 Map of the study area

Table 1. Approximate island size in hectares.*

Providence Island	61.24
Green Island	30.62
Island 2	7.66
Island 3	2.04
Long Island	2.04
Island 1	1.53
Round Island	1.04

*Computed from 1:15,000 aerial photographs using cm^2 paper over traced outline of treed area only. Willow flats were excluded.

Table 2. Approximate distance to nearest colonizing source (over ice) in metres.*

Providence Island to Meridian Island	480
Green Island to Mission Island	420
Island 2 to Meridian Island	600
Island 3 to island along the north shore	600
Long Island to Meridian Island	75
Island 1 to Big Poplar Island	75
Round Island to island along Meridian Island	150

*Measured from 1:60,000 aerial photographs.

was not possible within the scope of this study to measure such variation with the degree of refinement necessary to have any meaning in terms of the hypotheses.

Spring break-up

Measurements of snow characteristics and temperature were taken near Old Ferry Road throughout the preceding winter as part of a continuing study, the methods of which were described by Fuller *et al.* (1969). The last reading in the spring of 1973 was taken on 15 April, when snow depth was recorded at 30 cm, soil surface temperature at 0°C and air temperature at +5°C.

The sequence of ice break-up of the Mackenzie River was recorded by Salter *et al.* (1974) as follows: The first pools of melt-water on the ice surface and leads in the river ice occurred in the Fort Providence area during the last week of April, at which time ducks were first observed in the area. By 1 May there were areas of open water in the vicinity of Fort Providence. The river cleared slowly of ice during the next 14 days and was completely ice-free by 17 May. Subsequently, ice from Great Slave Lake (Beaver Lake), entering the Mackenzie River, completely filled the main channel at the ferry crossing by 21 May. After a few days the river was then ice-free once more.

METHODS

Snap-trapping

Trapping periods for different locations are shown in Table 3. Both Museum Special and Victor Mouse traps were used. Traps were baited with peanut butter and set for three consecutive nights. They were checked, re-baited and re-set as necessary on the first two mornings and picked up on the third.

On all trap lines, traps were set approximately 5 m apart, as measured by pacing. However, the length and number of lines varied according to island size and number of co-workers. Where parallel lines were run, these were spaced approximately 25 m apart. Where visibility was limited, direction was taken by compass bearings. On the mainland three parallel lines were run in June and two parallel lines were run at other periods. Two parallel lines were run diagonally across both Providence and Green Islands. Three parallel lines were run across Islands 1 and 3. A single line was run down the length of Long Island, and two parallel lines were run across Round Island. On Island 2 one line was run to encircle the island in June. The same direction and distance from the shoreline was maintained by keeping the edge of the tree canopy in sight. In August, approximately the same line was re-run and two parallel lines were run by compass to transect the island from west to east. On Islands 1 and 3 approximately the same lines were re-run in August. On Providence* and Green Islands and at Old Ferry Road,

*Only one (fairly straight) line was run on Providence Island in June. The second trapper became 'turned around' and set his traps in a corkscrew pattern in a relatively small area. The June sample for *C. rutilus* is probably therefore biased.

Table 3. Trapping periods for different locations.

Mainland			
Old Ferry Rd.	20-22 June	30 July - 1 Aug.	27-29 Aug.
Simpson Jct.			9-11 & 13-15 Aug.
Islands			
Providence Is.	14-16 June	23-26 July	19-21 Aug.
Green Island	14-16 June	30 July - 1 Aug.	19-21 Aug.
Island 2	17-19 June		6- 8 Aug.
Island 3	17-19 June		6- 8 Aug.
Island 1	17-19 June		6- 8 Aug.
Long Island			6- 8 Aug.
Round Island			6- 8 Aug.

trap lines were located in different areas in June and July, but in August some overlap of lines occurred with those that had been run in June. At Simpson Junction two different areas were trapped in August.

From 3,591 trap nights (TN) in June and 4,080 TN in August, indices of relative numbers were obtained. A further 2,398 TN in July provided additional material for autopsies. This effort yielded 844 individual cricetids, of which, 548 were *Clethrionomys rutilus*, 279 were *Peromyscus maniculatus*, 14 were *Microtus pennsylvanicus* and 3 were *Phenacomys intermedius*. In addition 36 individuals of *Sorex* spp. were collected and preserved, but not examined.

Two adjustments were applied to the raw data for calculating relative numbers. First, traps occupied by non-target species were assumed to have been unavailable to target species, and the number of TN was reduced accordingly. Second, sprung traps were assumed to have been available 50% of each night. The second adjustment made only a minor difference in population indices, no difference to the relative rank of any population, and no difference to statistical significance. Indices are accordingly presented without adjustment for sprung traps, and they are assumed to be representative of actual populations.

Autopsies

Data were collected in the field on duplicate sets of autopsy cards. All cricetids were measured to the nearest mm according to standard practice and weighed to the nearest 0.1 g. Weights of visibly pregnant females were adjusted by subtracting the weight of the reproductive tract, including embryos *in situ*. Pelts were removed and examined for presence and stage of moult and wounds. For males the length and width of testes and their position (scrotal or abdominal)

were recorded. Relative size of seminal vesicles was also noted. Presence of macroscopically visible tubules in the epididymis was taken as evidence of functional reproductive state and hence maturity (Fuller 1969). In cases where individuals had testes intermediate in size with tubules not prominent, smears were made of testis and epididymis and examined microscopically for presence of sperm. Females were examined to determine reproductive condition according to the methods of Tupikova (1964), with the exception that vaginal smears were not made. Presence of corpora lutea was taken as evidence of both maturity and pregnancy. In young animals, perforate vaginae and the presence of secondary follicles were taken as evidence of approaching maturity.

Reproductive tracts of all *C. rutilus* females whose body weight exceeded 11.9 g were removed intact and preserved in Bouin's fluid. Visible embryos were subsequently aged according to stage of development (Tupikova 1964). Skulls of all *C. rutilus* individuals were roughly cleaned, labelled, hung to dry in the field and subsequently returned to the University of Alberta where cleaning was finished by the larvae of dermestid beetles.

Age determination

The labial aspect of the second upper molar (M^2) of all *C. rutilus* individuals was exposed, either by flaking away the covering bone by scalpel, or by a dental drill fitted with a fine bit. The tooth was then examined under a Zeiss dissecting microscope and measurements were made to the nearest 0.1 mm by ocular micrometer at 10 x magnification.

Characteristic stages of growth were noted and compared with descriptions and photographs made by Tupikova *et al.* (1968). The length of the entire tooth was measured from the anterior edge of the occlusal surface as far proximally as development had proceeded (Figure 2). The anterior groove was considered closed if bridged by material of $\geq$ 0.1 mm thickness. Measurements were made from the point of closure of the anterior groove up the anterior side of the neck and anterior root, if present. No distinction was made between the neck and the anterior root, the amount of growth from the anterior groove being considered the more important factor. In the absence of any evidence to the contrary, it was assumed that there would be less individual variation in that rate of growth than in the amount of neck that was grown before the roots formed. By dividing the tooth into essentially two portions there was also less room for error in measurements. That portion of the tooth distal to the closed anterior groove (or if the anterior groove was open, the whole tooth) was considered to be the crown. In the case of individuals with an open M^2 groove, the first lower molar (M_1) was exposed and examined to determine whether the anterior groove of that tooth was open or closed.

Tupikova *et al.* (1968) stated that grooves of M^2 of *Clethrionomys* individuals closed at approximately 2 months and that a juvenile moult occurred in animals between the age of 25-30 days. Accordingly, primeness or moulting of the pelt of young animals (as determined from the inside of the exposed pelt), was correlated with stage of tooth development (Table 4) in order to relate those stages to chronological age.

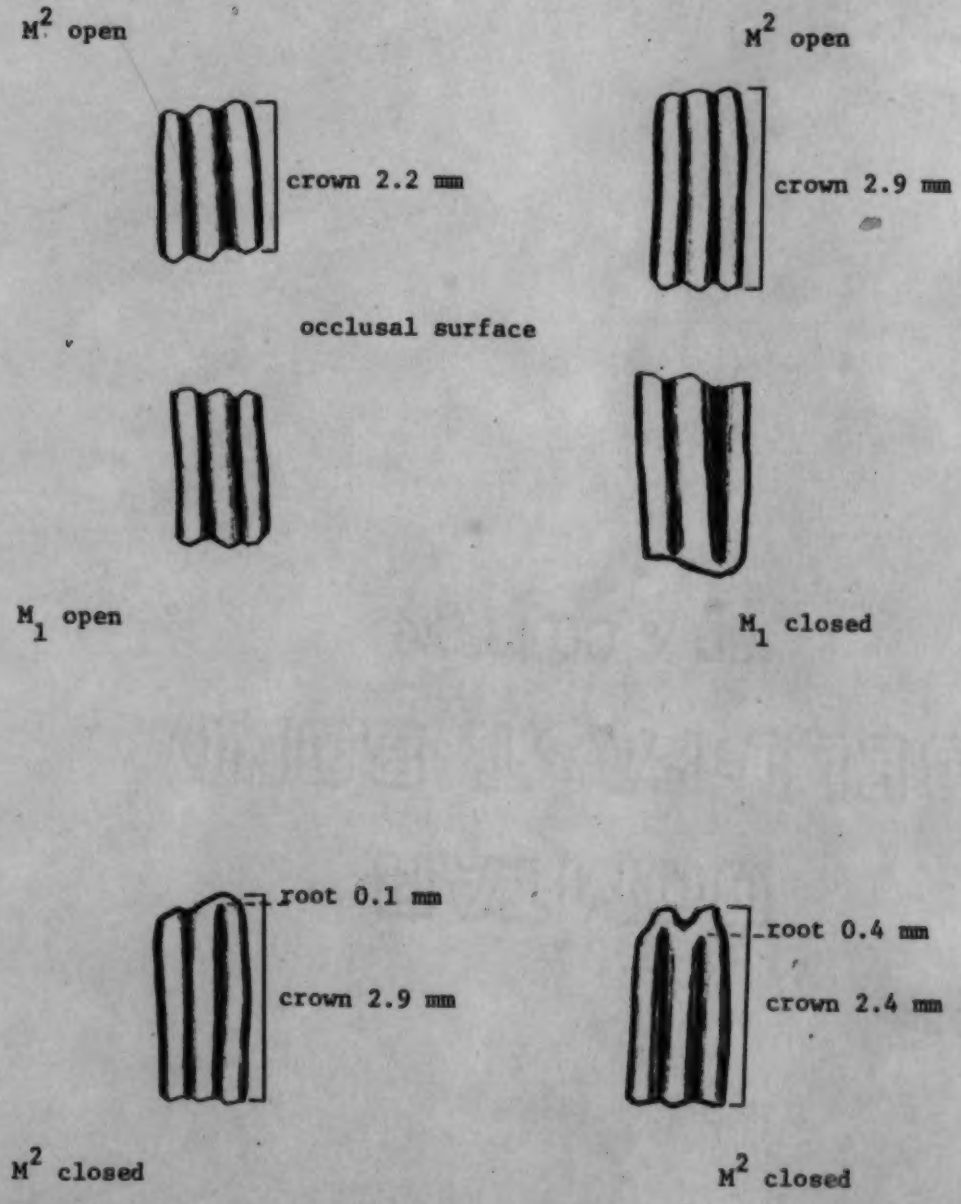


Figure 2 Sketches of the labial aspect of the first lower molar (M_1) and the second upper molar (M^2) at different stages of development, showing points of measurement. (Anterior groove on the right. Magnification X 10).

Table 4. Percentage of animals with prime pelts at different stages of tooth development. (n) = sample size.

	Stage of tooth development		
Period	M_1 open	M_1 closed	M^2 root length 0.1 mm
June	(17) 88.2%	(15) 46.7%	(2) 50.0%
Late July	(9) 77.8%	(11) 18.2%	(23) 65.2%
Mid August	(32) 94.0%	(73) 35.6%	(84) 78.0%
Late August	(14) 64.3%	(41) 15.1%	(38) 57.2%
All periods combined	(72) 84.7%	(140) 30.0%	(147) 70.0%

TREATMENT OF DATA

Statistical analysis

Statistical analysis of data followed procedures described by Sokal and Rohlf (1969). The basic assumption was that relative numbers of animals (catch/100 TN) were representative of population size. A second assumption was that animals of any island were considered to belong to one population, regardless of island size. Similarly, animals from each of the two mainland locations were considered to belong to only two populations. An attempt was made to avoid the concept of density as far as possible. Anderson (1970) noted the dangers of considering a population "as any group of animals specified by an investigator". Sadleir (1969) described the inadequacy of the concept "density" as a measure of social pressure, since differences in heterogeneity of environments are not considered. Both points are well taken, but we have some way to go yet in perfecting the necessary complexity of non-destructive measurements that would allow avoidance of these hazards of thought in field studies of small rodents.

RESULTS

Relative numbers

Indices of relative numbers in June and August are shown for all cricetids and for *C. rutilus* and *P. maniculatus* separately in Table 5. The hypothesis of negative correlation of population with island size (mainland being considered the largest island in rank) was first tested by Spearman's rank test which showed no statistical significance in differences between populations. However, since this test is designed for large sample sizes the data were also submitted to a chi square 2 x n contingency test. The results of that analysis failed to show significance in expected relative numbers as related to island size (Figures 3 and 4). However, the analysis does show that Island 2 and Island 1 consistently had the largest populations (Figures 3 and 4). Only in the case of all cricetids in August did any other population exceed that of Island 2. Similarly the mainland area of the Old Ferry Road showed populations that were consistently either lowest or not significantly different from the lowest populations.

The results of this analysis show that adjacent islands have populations that are in some cases significantly different from each other, but that the difference is not necessarily related to the parameter of island size. The analysis further suggests a secondary hypothesis that the relative numbers of *C. rutilus* and/or all cricetids are greater on islands of approximately 60 ha or less than on mainland. A modified Student's t-test of one observation (mainland) against a sample (islands) was used to test this hypothesis but failed to show significance.

Table 5. Animals caught per 100 trap nights in June and August.

	C. rutilus		*P. maniculatus*		Cricetidae	
Location	June	August	June	August	June	August
Round Island	-	6.0	-	9.2	-	14.2
Island 1	5.0	18.5	1.0	0.0	6.8	19.0
Long Island	-	7.6	-	0.5	-	8.3
Island 3	2.4	8.5	0.5	0.0	2.9	8.5
Island 2	6.0	22.0	3.1	0.0	8.7	22.5
Green Island	2.7	15.9	1.9	2.4	4.7	17.8
Providence Is.	0.7	14.3	3.1	13.0	4.4	24.0
Old Ferry Rd.	1.0	4.1	0.3	2.6	1.3	6.7
Simpson Jct.	-	3.8	-	6.2	-	9.6

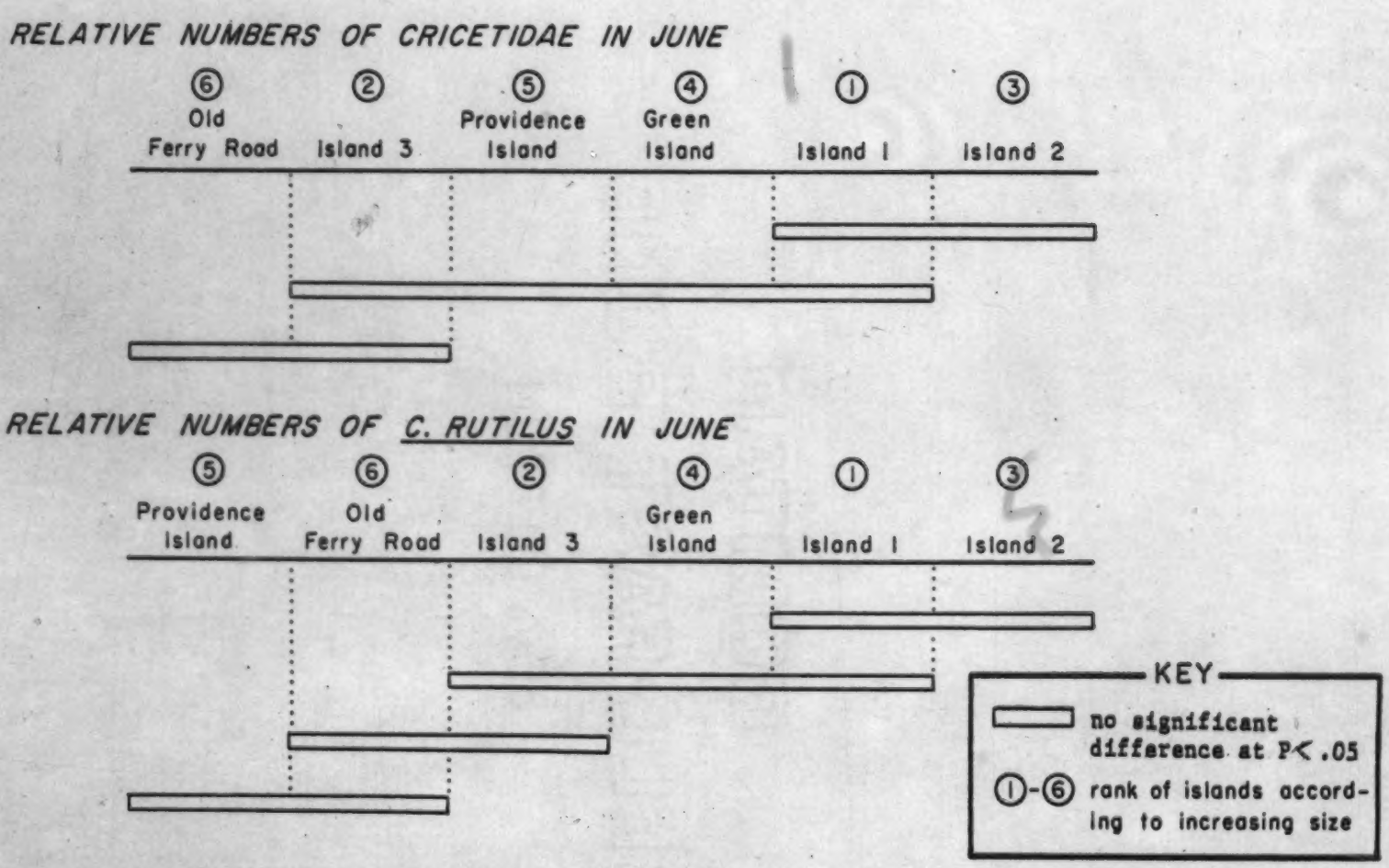


Figure 3 Analysis of relative numbers of populations by chi square 2 x n contingency test in June

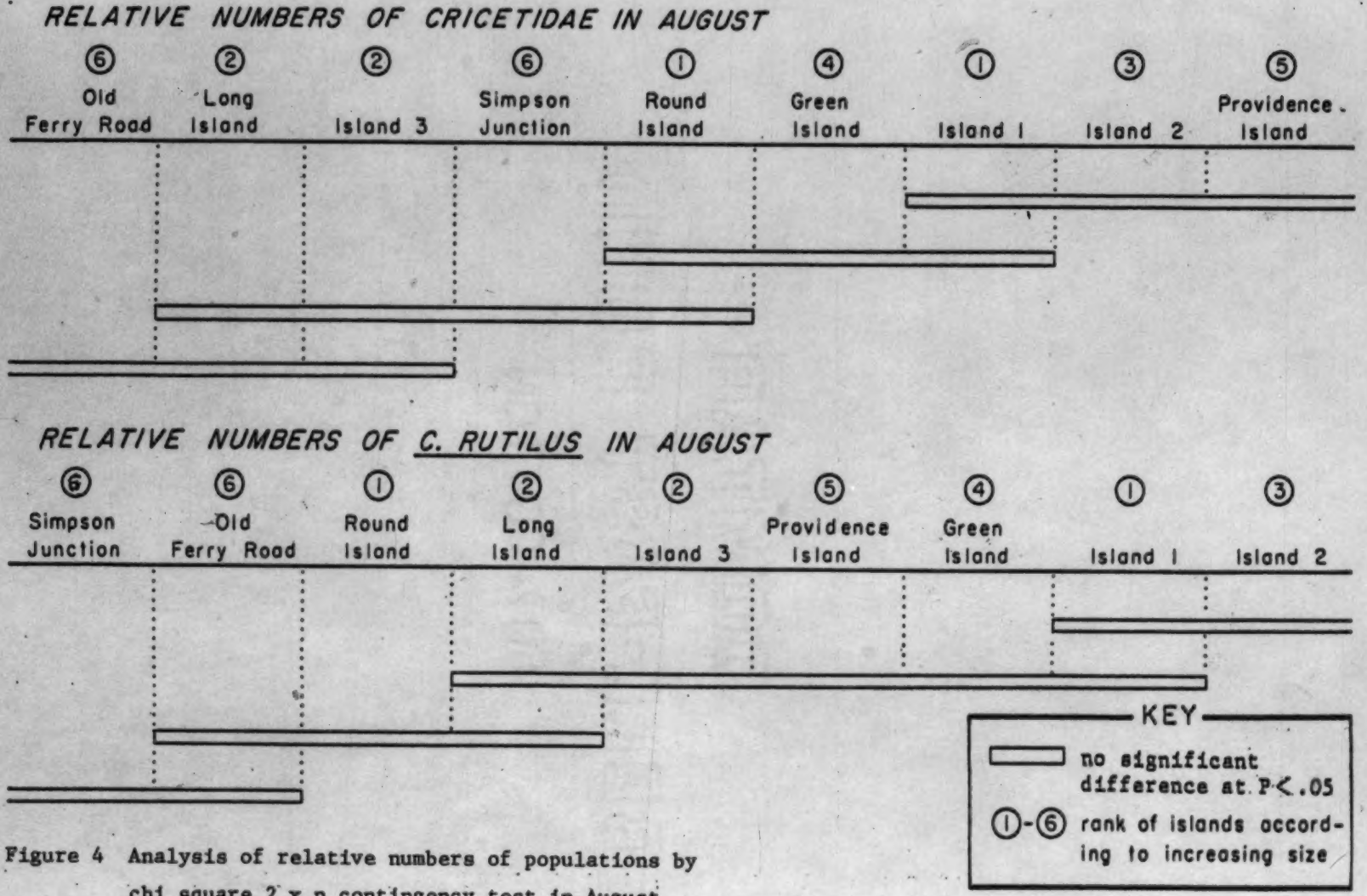


Figure 4 Analysis of relative numbers of populations by chi square 2 x n contingency test in August

Due to logistical problems the time required to trap all islands in August was 21 days as compared to 6 days in June (Table 3). Pregnant *C. rutilus* females were present in six of the nine populations that were sampled in August. The exceptions were Round Island, Island 1, and Old Ferry Road. The last-named population was trapped last in the series (August 27-29). In an attempt to compensate for this 21 day period, indices were extrapolated or interpolated to 15 August (Figures 5 and 6). The indices for Simpson Junction are also shown in these figures, since the mid point of the trapping session at this location fell on 13 August. If the adjusted data are accepted as being closer to the actual populations in mid August than those compared over a 21 day period, then the mainland populations of *C. rutilus* were substantially lower than those of the islands. In the case of cricetids (Figure 6), the populations of Island 3 and Simpson Junction were almost equal, while those of the other islands were again higher and that of Old Ferry Road was again the lowest.

Comparative rate of population increase

The instantaneous rate of population increase (R) from June to August was calculated from the following formula:

$$\frac{\ln \frac{n(t)}{n(o)}}{t} = R$$

Where: ln = natural logarithm

n(t) = number of young of the year/100 trap nights at the mid-points of the August trapping periods

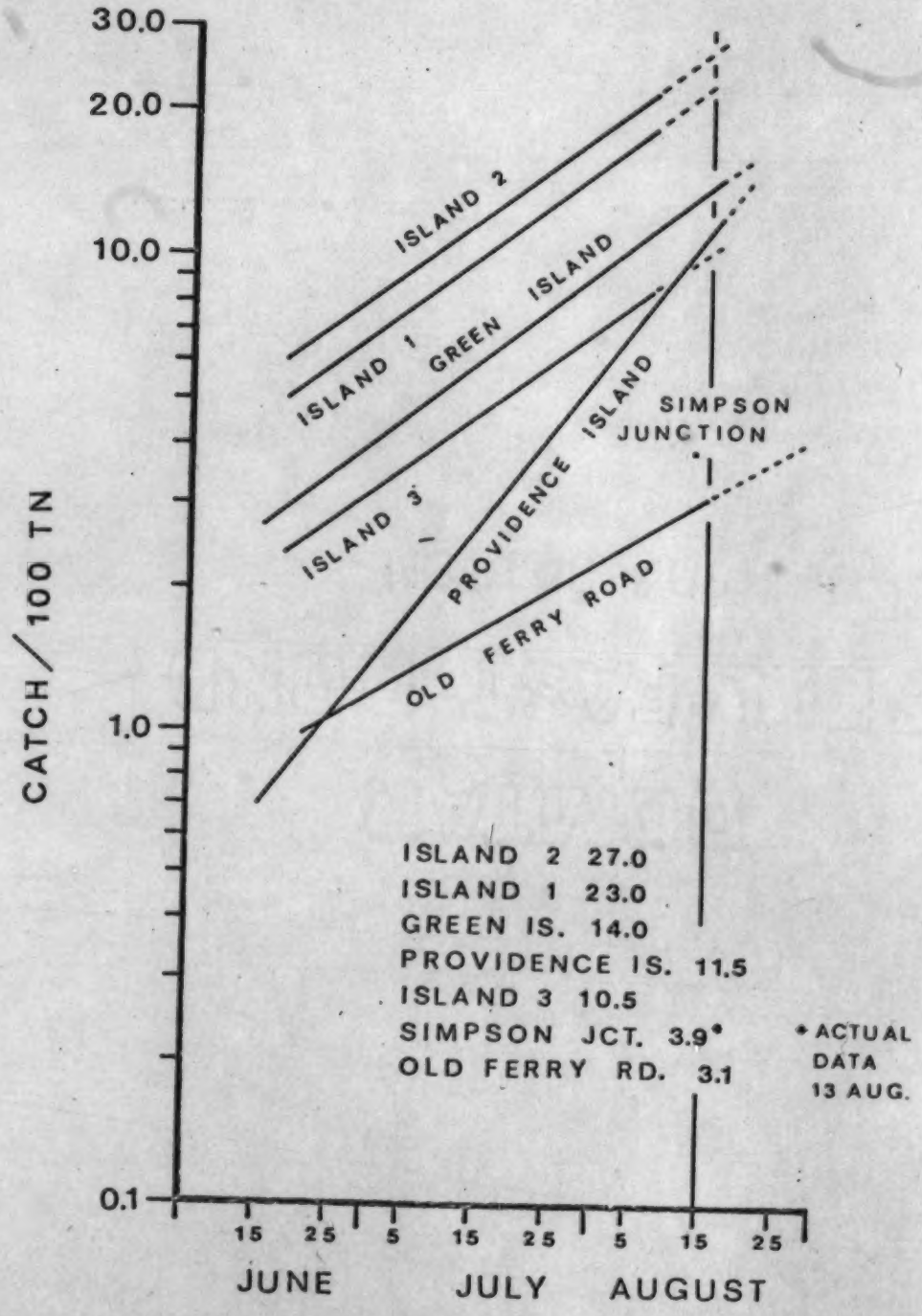


Figure 5 Extrapolated or interpolated indices of populations of *C.rutilus* in mid August, assuming exponential growth

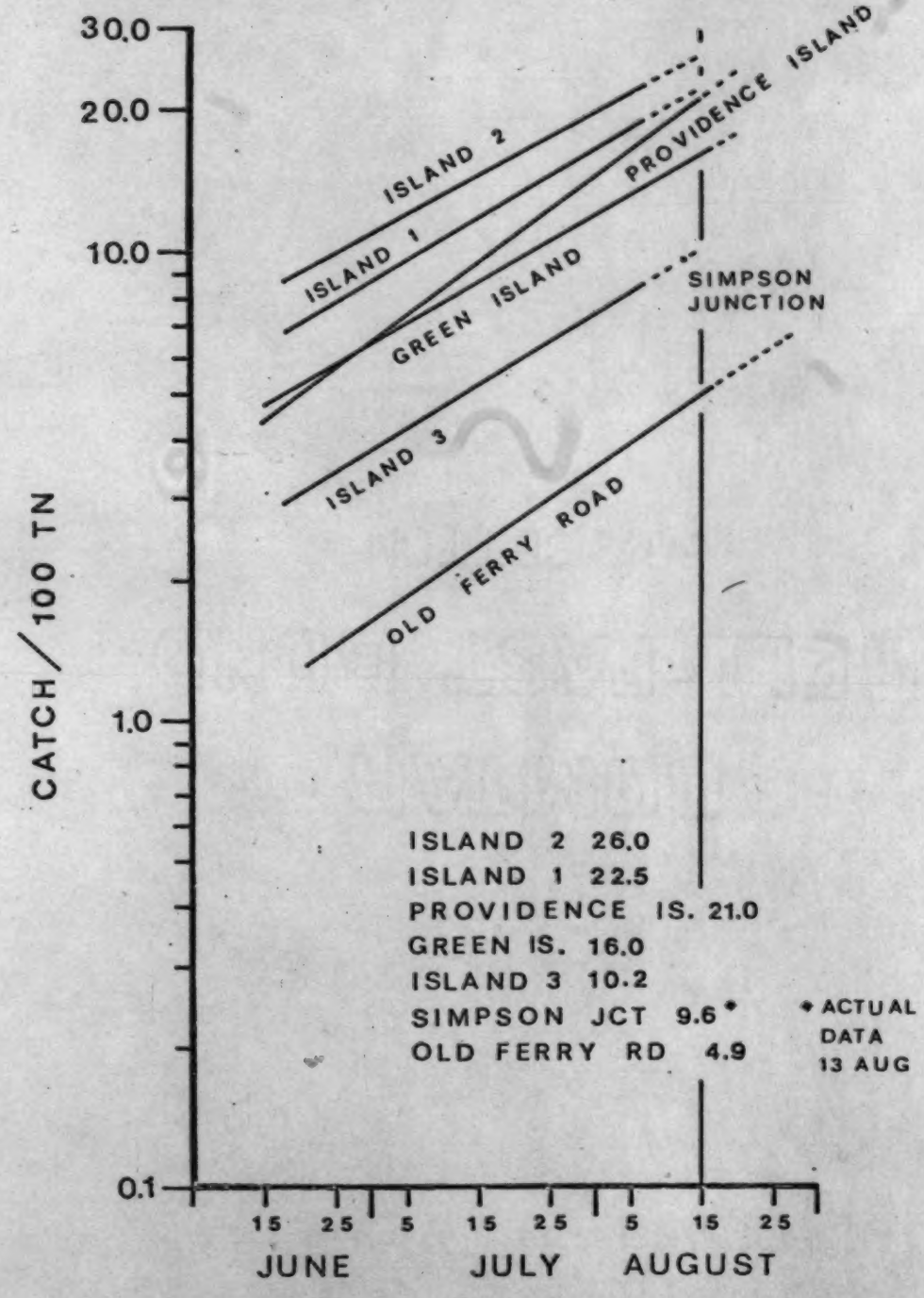


Figure 6 Extrapolated or interpolated indices of populations of Cricetidae in mid August, assuming exponential growth

n(o) = number of overwintered (OW) females/100 trap nights at the mid-points of the June trapping periods

t = time in days between the mid-points of each June and August trapping period.

Instantaneous rate of increase for cricetids in island populations shows a weak negative correlation with the number of OW females in June (Table 6). There is no consistent positive or negative correlation with island size. On Island 2, *P. maniculatus* went to apparent extinction (Table 6).

Division of age classes

Because of the necessity of assigning ages to young of the year with the greatest precision possible, the rationale for such assignment is presented below in some detail.

Morphological characteristics

Morphological characteristics in the sequence of development of molar teeth of *C. rutilus* are readily observed and measured, and animals are grouped according to those characteristics. In this study they are: closure of the anterior groove of M_1; closure of the anterior groove of M^2; and root length of M^2. In all animals examined, closure of the anterior groove of M_1 occurred before that of M^2. Animals with M^2 open had an M^2 length that ranged from 2.1-3.4 mm (Figure 7). This range appeared to be greater than would be accounted for by individual variation. Both the teeth and alveolar bone of five animals with an M^2 length of 2.1-2.3 mm were very fragile. (Increased density of bone and increased hardness of teeth occurs with increased age.) Most animals

Table 6. Pearson correlation coefficients (r) between the number of OW females and instantaneous rate of population growth.

Location	No. OW females/ 100 TN in June	Young/ female/day	r	Significance
C. rutilus				
Island 2	1.9	.048		
Green Is.	1.4	.036		
Island 1	0.9	.060		
Island 3*	0.5	.057		
Providence Is.+	0.3	.057		
Old Ferry Rd.	0.3	.038		
Means of islands alone			-0.653	ns
Means of islands plus mainland			-0.262	ns
P. maniculatus				
Island 2	2.0	.000		
Providence Is.	1.7	.029		
Green Is.	1.2	.009		
Islands 1 & 3	0.0	-		
Old Ferry Rd.	0.1	.044		
Cricetidae				
Island 2	3.8	.035		
Green Is.	2.7	.028		
Providence Is.	2.1	.036		
Island 1	1.0	.059		
Island 3*	0.5	.057		
Old Ferry Rd.	0.4	.039		
Means of islands alone			-0.843	.037
Means of islands plus mainland			-0.666	ns

*No females captured but one female assumed since young animals were taken in June.

+Biased sample (see Methods). Probably more OW *C. rutilus* females were present than are indicated.

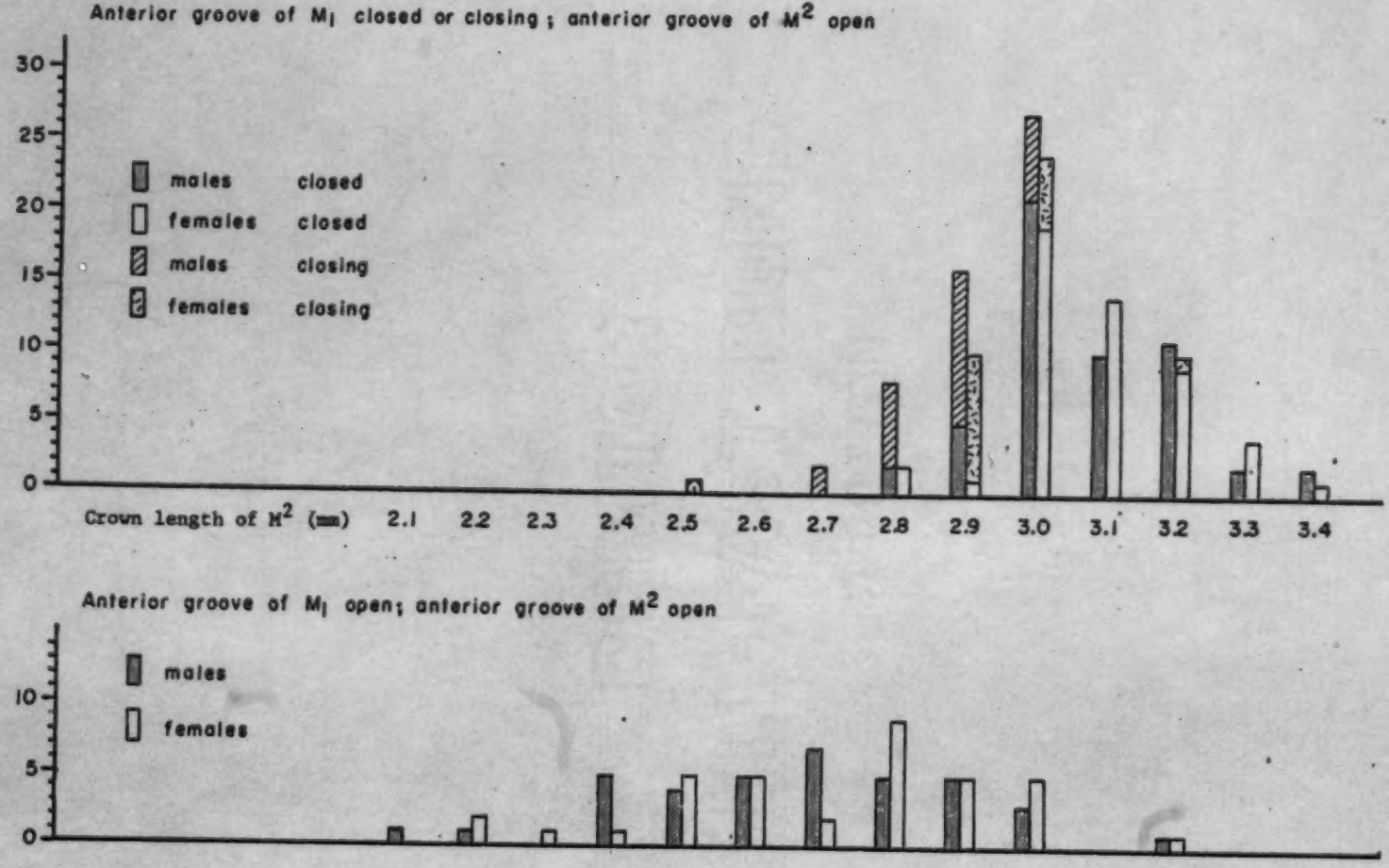


Figure 7 Distribution of the number of voles achieving closure of the anterior groove of M_1 at different M^2 lengths

with M_1 open had an M^2 length that was less than 3.0 mm (Figure 7, lower), whereas most animals with M_1 closing or just closed had an M^2 length that was 3.0 mm or more (Figure 7, upper). Therefore the length of the M^2 in *C. rutilus* increases from weaning until closure of the anterior groove of the M^2, which latter event is preceded by closure of the anterior groove of the M_1.

Overwintered animals were easily distinguished from young of the year on the basis of root growth of M^2. In June and July root length ranged from 1.1-2.6 mm in overwintered animals, and in August from 1.5-2.2 mm. Since all overwintered animals were sexually active no attempt was made to distinguish sub groups within this class. In contrast, animals trapped in July with a maximum root length of 0.3 mm were clearly young of the year. In August, root length of such animals attained a maximum of 0.8 mm.

Factors to be considered in assignment of ages

Assignment of ages, in weeks or days, to younger groups can be made by continuous sampling throughout the breeding season to detect appearance, peak and disappearance of morphologically distinct groups, and such data can be compared with first and last litters of the season. This method, however, requires frequent and large samples. Mean birth dates can also be calculated and animals assigned to cohorts from the age of embryos of pregnant females, but if the samples also include many females with placental scars this method may be misleading. From examination of the uterus, date of parturition cannot be estimated with accuracy after four or five days (Tupikova 1964). Presence of females with placental scars will therefore shift the mean birth date back in time and make assignment of animals to cohorts less reliable.

In assigning ages to groups of animals it is also recognized that the effect of daylength, temperature and nutrition on tooth growth and especially on hormonal mediation of tooth growth in relation to reproduction is not at present known for any microtine. Rates of attrition of the occlusal surface of the crown are largely dependent on amount and quality of food intake and thickness of enamel. The question of stimulation of proximal growth by the process of attrition affords another factor of variability. Nevertheless, the question of reproduction of young of the year can hardly be illuminated unless these animals can be placed with a fair degree of confidence into age groups. Therefore two possibilities have to be evaluated. The first possibility is that seasonal changes, which are known to affect growth and differentiation of certain organs and tissues (Schwarz *et al.* 1964), and body composition (Fedyk 1974), may also affect tooth growth *from June through August* to the extent that assignment of animals to age groups during this time, carries too great a margin of error. The second possibility is that the condition of sexual maturity itself, and particularly pregnancy, is associated with increased tooth growth to the extent that any argument for acceleration or inhibition of sexual maturation would be a circular argument. This latter point will also be discussed in a later section.

Seasonal differences

Koshkina (1955) observed that, under natural conditions, root growth of *C. rutilus* on the Kola Peninsula (68° 00'N) slows in August. Fuller (pers. comm.) observed the same phenomenon in the Northwest Territories (61° 00'N) by mid October. Martell (pers. comm.) observed that root growth of *C. rutilus* in the Mackenzie Delta (69° 00'N), while very slow, continued throughout the winter, whereas bone growth ceased

completely. Tupikova and co-workers collected the majority of their material for analysis from May through August at a latitude of approximately 50° 00'N but did not observe any slowing of root growth by the end of the season, although they recognized the possibility in the case of autumn born animals.

Because of other variables to be considered in mature young of the year, seasonal differences in tooth growth were only considered in sexually immature animals. No significant difference was found in M^2 crown length between males and females in June or August, or within the sexes between those months (Table 7). Samples were taken in August only from those populations which had also been sampled in June in order to reduce genetic bias as much as possible. Since only two males with M^2 closed (roots 0.1 mm) were taken in June, comparison of animals in that category could only be made between samples from Green and Providence Islands in late July and August. Comparison of mean total M^2 length showed no significant difference between months, but there was a sexual difference in August ($P < .05$, Table 7).

Because bone and dentin are histologically relatively similar, are of similar chemical composition, and are both derived from mesoderm, bone growth and tooth growth were compared to ascertain whether growth responses to seasonal environmental changes might also be similar. Significant differences were found in body length between young in the first three groups (Table 8), M_1 open; M_1 closed; M^2 roots 0.1 mm; but no significant difference in body length between groups with root growth of 0.1 mm, 0.2 mm and 0.3 mm. By August, therefore, body growth in length had apparently ceased in non-reproductive animals by the time of closure of M^2, while root growth still continued. These results suggest that expression of M^2 growth in young animals is not affected by seasonal

Table 7. Comparison of M^2 mean crown length in non-reproductive animals according to month and sex. (Animals with M_1 open not included.)

Month	Group	Sex	Crown Length $\bar{x} \pm SE$	(n)	Significance
June	M^2 open	male	2.98 ± .036	(10)	ns
August	M^2 open	male	3.01 ± .156	(57)	
June	M^2 open	female	3.03 ± .021	(6)	ns
August	M^2 open	female	3.05 ± .021	(42)	
July	M^2 roots 0.1 mm	male	2.94 ± .034	(12)	ns
August	M^2 roots 0.1 mm	male	2.96 ± .034	(14)	
July	M^2 roots 0.1 mm	female	2.70 ± -	(1)	-
August	M^2 roots 0.1 mm	female	3.06 ± .022	(20)	

ns (June/August open, male/female); ns (open/roots, male/female); ns (open/roots, July/August); P < .05 (July/August roots, female/male)

Table 8. Relationship of body length (mm) to tooth characteristics in non-reproductive animals in August only.

Group	Mean Length ± SE	Range	(n)	Significance
M_1 open	77.7 ± 0.79	70.0 - 89.0	(45)	
				P < .001
M_1 closed	84.2 ± 0.63	62.0 - 95.0	(I12)	
				P < .001
M^2 roots 0.1 mm	89.3 ± 0.50	74.0 - 99.0	(115)	
				ns
M^2 roots 0.2 mm	89.5 ± 1.51	75.0 - 97.0	(17)	
				ns
M^2 roots 0.3 mm	87.7 ± 2.09	87.0 - 96.0	(7)	

changes from June through August. They do not, however, indicate whether this expression is achieved in August in the same number of days as in June.

Inter-sexual differences

Means for total M^2 length for each root length category were tested separately for males and females by Duncan's multiple range test (Table 9). Females showed little heterogeneity at $P < .05$. Non-reproductive males with roots of 0.1 mm were significantly different from other categories at $P < .05$. Inter sexual differences in crown height and crown wear are shown in Table 10. Males showed greater attrition than females between M^2 root lengths of 0.1 and 0.2 mm regardless of whether they were sexually mature or not.

M^2 lengths of males and females of the same root length category were compared by Student's t-test. Non-reproductive females with M^2 root of 0.1 mm were significantly ($P < .001$) longer than those of male counterparts. There are three possible explanations for this difference. First, that females may have a more rapid rate of M^2 growth than males before closure of the anterior groove; second, that males may have the same rate of growth, but a greater rate of attrition than females at this stage; and third, that M^2 closure, being a phenomenon of morphological differentiation as well as of growth, may take place at an earlier age in males than in females. Eruption of teeth is largely a function of levels of thyroxine (Gorbman *et al.* 1962). The hormonal basis for differentiation is not clear. However, in a study of root growth in *C. glareolus*, Lowe (1970) reported that males formed roots earlier than females and also that differences in reproductive condition

Table 9. Significance of differences (Duncan's multiple range test) between mean M^2 lengths according to root growth categories. Data underlined are not different at the $P < .05$ level of significance. (All months combined).

				Reproductive			
Females							
M^2 root length mm	0.1	0.2	0.3	0.1	0.2	0.3	0.4-0.8
$\bar{X}$ M^2 length mm	3.15	3.12	-	3.09	3.01	2.94	2.94
Males							
M^2 root length mm	0.1	0.2	0.3	0.1	0.2	0.3	0.4-0.5
$\bar{X}$ M^2 length mm	3.06	2.93	2.93	2.93	2.79	2.74	2.70

Table 10. Attrition of M^2 crown in relation to root growth (mm).

					— Reproductive —		
Females							
M^2 root length	0.0	0.1	0.2	0.3	0.1	0.2	0.3
$\bar{X}$ M^2 crown length	3.06	3.05	2.99	-	2.99	2.81	2.64
Attrition		.01	.06			.18	.17
Males							
M^2 root length	0.0	0.1	0.2	0.3	0.1	0.2	0.3
$\bar{X}$ M^2 crown length	3.01	2.96	2.73	2.63	2.83	2.59	2.44
Attrition		.05	.23	.10		.24	.15

had an effect on tooth growth and differentiation. These data have yet to be published. Consequently, consideration in the present study was given primarily to assigning chronological ages to females. This was done not only because of the apparent sex difference, but also because apparent ages of mature females can be checked against reproductive evidence. While errors of interpretation can be made, such evidence can in most cases give at least a minimum age.

Rates of early tooth growth

Martell (1975) observed that young of *C. rutilus* were weaned and first emerged from their nest at 15-16 days, at which time the mean M^2 length was 2.0 mm. The smallest animals that were trapped in the present study had an M^2 length of 2.10-2.30 mm and were assumed to have been recently weaned. Morrison *et al.* (1954) found that temperature regulation in *C. rutilus* was fully developed by about 18 days, although the average body temperature did not equal that of adults until about 28 days. Gebczynski (1975) found that body temperature of *C. glareolus* increased steadily from the tenth to the nineteenth day of life, at which time it reached the adult level of 37-39°C. Young would therefore be more readily trappable by about the eighteenth day of life. Martell (1975) measured M^2 growth from weaning until 30 days in laboratory raised animals and recorded a mean M^2 length of 2.60 mm at 20 days, which gives a growth rate of 0.120 mm/day (i.e. 0.60 mm in 5 days) Animals in the present study with M_1 open had a mean M^2 length of 2.62 mm (n = 73). They also showed a fairly high correlation with the age criterion of pelt condition (Table 4) at less than 25 days. Young with M_1 open and an M^2 length of about 2.60 mm were therefore considered to be approximately 20 days old. They were clearly distinct from females

with M_1 closed. The latter group had a mean M^2 length of 3.06 mm (n = 60), which corresponded with Martell's measurements of animals aged 25 days and 30 days and having a mean length of 3.02 and 3.04 mm respectively. A high percentage of these M_1 closed females were also undergoing a juvenile moult (Table 4). Mean body length differed in this group between animals with M_1 open and with immature animals with M^2 closed at a significance of $P < .001$ in both cases (Table 8). This group was therefore considered to be 25-30 days old. Net rate of M^2 growth/day between M_1 open and M_1 closed females was calculated at .092-.046 mm (i.e. 0.46 mm in 5-10 days).

Seasonal age classes

Cohorts *in June* were accordingly grouped into age classes as follows:

Criteria		Age Class
root length greater than 1.0 mm	=	overwintered (OW)
M_1 closed	=	25-30 days; early summer young (S_1)
M_1 open	=	17-24 days; early summer young (S_1)
nestlings (assumed from presence of lactating females with scars)	=	1-16 days; early summer young (S_1)
visible embryos (aged to day of birth)	=	minus 16-minus 1 day; mid summer young (S_2)

The above classification means that both the first and second litters of an OW female could be included in the S_1 age class and that all the young in this class either have been weaned or, in the case of nestlings, will be weaned before the end of the first week in July. Embryos would be weaned at the end of, or after the first week in July

and, together with subsequent litters weaned before the end of July are classed as S_2 young. Any litters weaned after July are classed as S_3 young. S_1, S_2 and S_3 are therefore seasonal age classes corresponding to early summer, mid-summer and late summer.

Since no data were available for known-age animals with M^2 closed, approximate chronological ages were calculated for females of three different populations in July and August on the basis of reproductive data. The ages were then checked against cohorts present in each population during the June trapping period and rates of growth were calculated for females having attained full M^2 length prior to closure of the anterior groove. With three exceptions the net rate of root growth varied from 0.010-0.015 mm/day (Figure 8). The same rate of growth was assumed for males.

Reproductive young of the year that were sampled in July all had either no roots or had M^2 roots of 0.3 mm or less, and no young of the year female had more than one set of placental scars. These data suggest that M^2 root growth is not increased by pregnancy, but is, within the limits of the season, a function of age. Further data in support of this conclusion will be given in a later section on body length and weight.

Population structure and reproductive status

In August no significant difference was found by chi-square analysis in the ratio of total males to total females (Table 11). However, there was deviation from the expected 1:1 ratio within age classes. Most striking was the virtual absence of males within the S_1 class, with the exception of that class in the Simpson Junction

Figure 8 Rate of root growth estimated after attainment of full crown length at approximately .010 - .015 mm/day, with age classes assigned in July and August accordingly. Numbers include males and females grouped according to stage of development at time of trapping. A = Islands 1, 2 and 3, Green Island, Providence Island and Old Ferry Road; B = Green Island, Providence Island and Old Ferry Road; C = Islands 1, 2 and 3. Long Island, Round Island and Simpson Junction; D = Green Island and Providence Island, and E = Old Ferry Road.

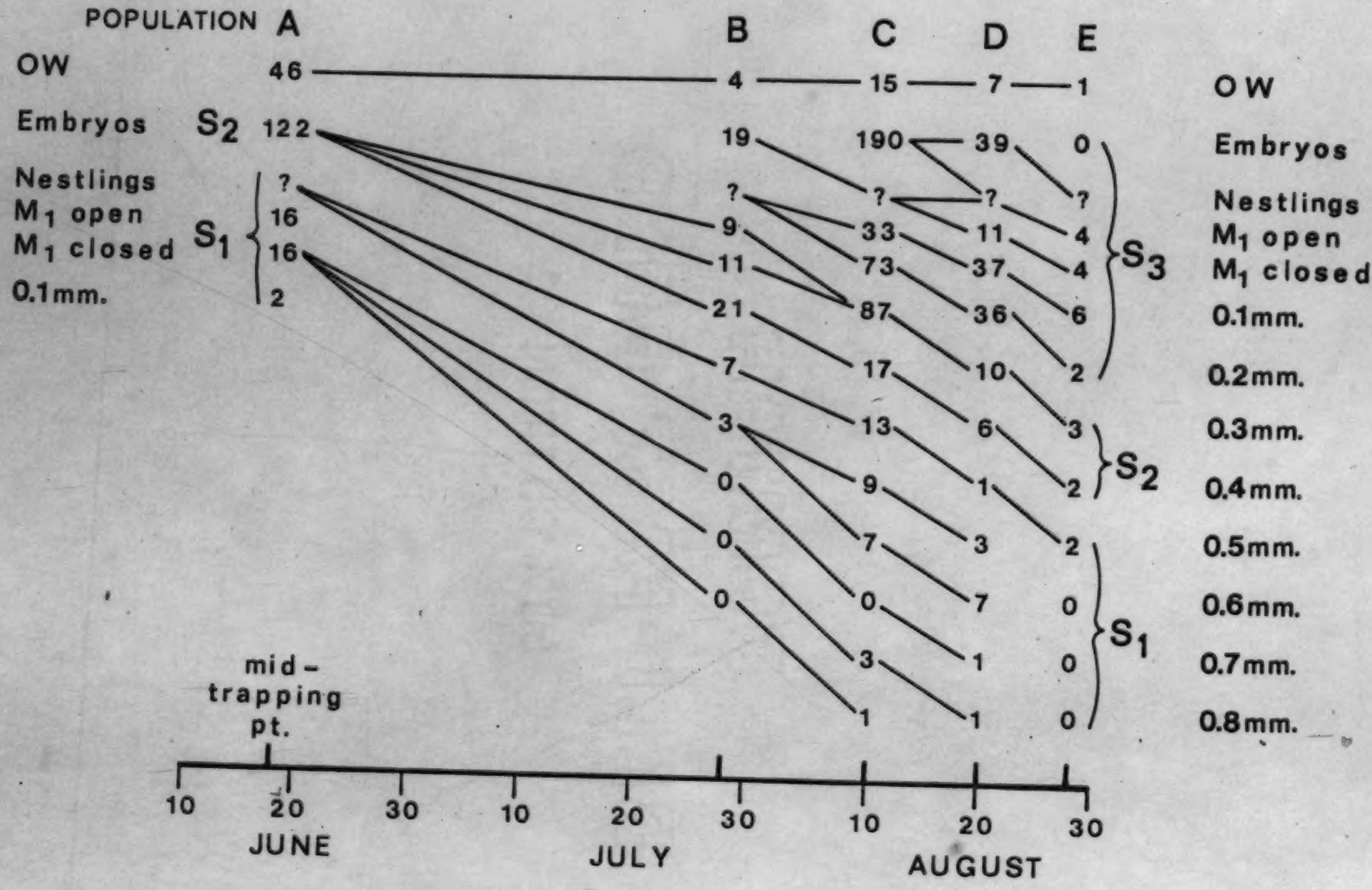

POPULATION
A
B
C
D
E
OW
Embryos
Nestlings
M1 open
M1 closed
0.1mm.
S2
S1
46
122
?
16
16
2
4
15
7
1
19
?
9
11
21
7
3
0
0
0
190
?
33
73
87
17
13
9
7
0
3
1
39
?
11
37
36
10
6
1
3
7
1
1
0
?
4
4
6
2
3
2
2
0
0
0
S3
S2
S1
OW
Embryos
Nestlings
M1 open
M1 closed
0.1mm.
0.2mm.
0.3mm.
0.4mm.
0.5mm.
0.6mm.
0.7mm.
0.8mm.
mid-trapping pt.
10
20
30
10
20
30
10
20
30
JUNE
JULY
AUGUST

Table 11. Sex ratios in August. Sample size is the first number in each column. Percentage of males is the second number.

Populations	OW		S_1		S_2		S_3		Total	
	(n)	%	(n)	%	(n)	%	(n)	%	(n)	%
Island 1	(0)	-	(1)	100.0	(21)	66.7	(8)	62.5	(30)	66.7
Round Island	(2)	50.0	(1)	0.0	(4)	25.0	(3)	33.3	(10)	30.0
Island 3	(0)	-	(3)	0.0	(5)	80.0	(7)	42.9	(15)	46.7
Long Island	(1)	100.0	(1)	0.0	(7)	28.6	(8)	50.0	(17)	41.2
Island 2	(7)	42.9	(18)	16.7	(45)	60.0	(70)	58.6	(140)	52.9
Green Island	(5)	60.0	(9)	0.0	(8)	87.5	(45)	44.4	(67)	44.8
Providence Is.	(5)	80.0	(4)	0.0	(8)	50.0	(39)	48.7	(56)	48.2
Old Ferry Rd.	(1)	100.0	(2)	0.0	(5)	40.0	(10)	40.0	(18)	38.9
Simpson Jct.	(2)	0.0	(9)	55.5	(22)	63.6	(10)	50.0	(43)	55.9
Total	(23)	56.5	(48)	18.8	(125)	60.0	(200)	51.0	(396)	51.8

population. In the total S_2 class an excess of males was significant at $P < .05$. When ratios are considered for June, July and August according to M^2 development a similar pattern is seen. Animals with M^2 open show an equal sex ratio in each month. A higher ratio of males with 0.1 mm roots occurs in July and with 0.2 mm roots in August. Males with M^2 roots greater than 0.5 mm are absent in August (Table 12). OW males formed 41.3% of the total OW population (n = 46) in June, while in August they formed 56.5% (n = 23).

Young of the year matured at an earlier age in June and July than in August (Table 13) and a greater proportion of females matured than males. All S_1 females were sexually mature, while two out of nine S_1 males had not matured by mid August (Figure 9). Only one S_3 female matured and no S_3 males. The proportion of S_2 animals that matured varied in different populations (Figure 9). There was no correlation between the percentage of mature S_2 males or females in August and the number of OW animals in June (Table 14), nor of OW and S_1 animals in August (Table 15).

Finally, there was a striking difference between the number of litters produced by OW females on Island 2 compared to those on Green Island. That this difference is not an artifact of sample size is supported by the presence of at least two cohorts of weaned young in June on Island 2 and only one on Green Island (Figure 10). Insufficient animals were trapped in other populations to allow comparison to be made.

Table 12. Sex ratios of young of the year in June, July, and August according to M^2 development. Sample size is the first number in each column. Percentage of males is the second number.

M^2 root growth in mm	June		July		August	
	(n)	%	(n)	%	(n)	%
0.0	(34)	52.9	(19)	52.6	(162)	54.3
0.1	(2)	100.0	(23)	73.9	(129)	54.3
0.2	-		(7)	71.4	(29)	65.5
0.3			(4)	75.0	(22)	50.0
0.4			-		(12)	25.0
0.5					(12)	8.3
0.6					(7)	0.0
0.7					(4)	0.0
0.8					(2)	0.0
Total young of year	(36)	55.6	(53)	66.0	(373)	49.9

Table 13. Seasonal differences in sexual maturation of young of the year in relation to M^2 development. (n = sample size, % = mature animals). Animals with M_1 open not included.

Month	M_2 root growth in mm	Males (n)	Males %	Females (n)	Females %
June	0.0	(10)	0.0	(6)	0.0*
	0.1	(2)	100.0	(0)	-
July	0.0	(4)	0.0	(7)	42.9x
	0.1	(17)	23.6	(6)	83.5
	0.2	(5)	80.0	(2)	50.0
	0.3	(2)	50.0	(1)	100.0
August	0.0	(64)	0.0	(50)	0.0
	0.1	(70)	4.3	(59)	17.0
	0.2	(19)	26.3	(10)	60.0
	0.3	(11)	36.4	(11)	100.0
	0.4	(3)	100.0	(9)	100.0
	0.5	(1)	100.0	(11)	100.0
	0.6	(0)	-	(7)	100.0
	0.7	(0)	-	(4)	100.0
	0.8	(0)	-	(2)	100.0

*50.0% had perforate vaginae and secondary follicles and were approaching estrus.

x28.6% had perforate vaginae and secondary follicles and were approaching estrus.

Figure 9 Population structure and reproductive status of *C.rutilus* in August

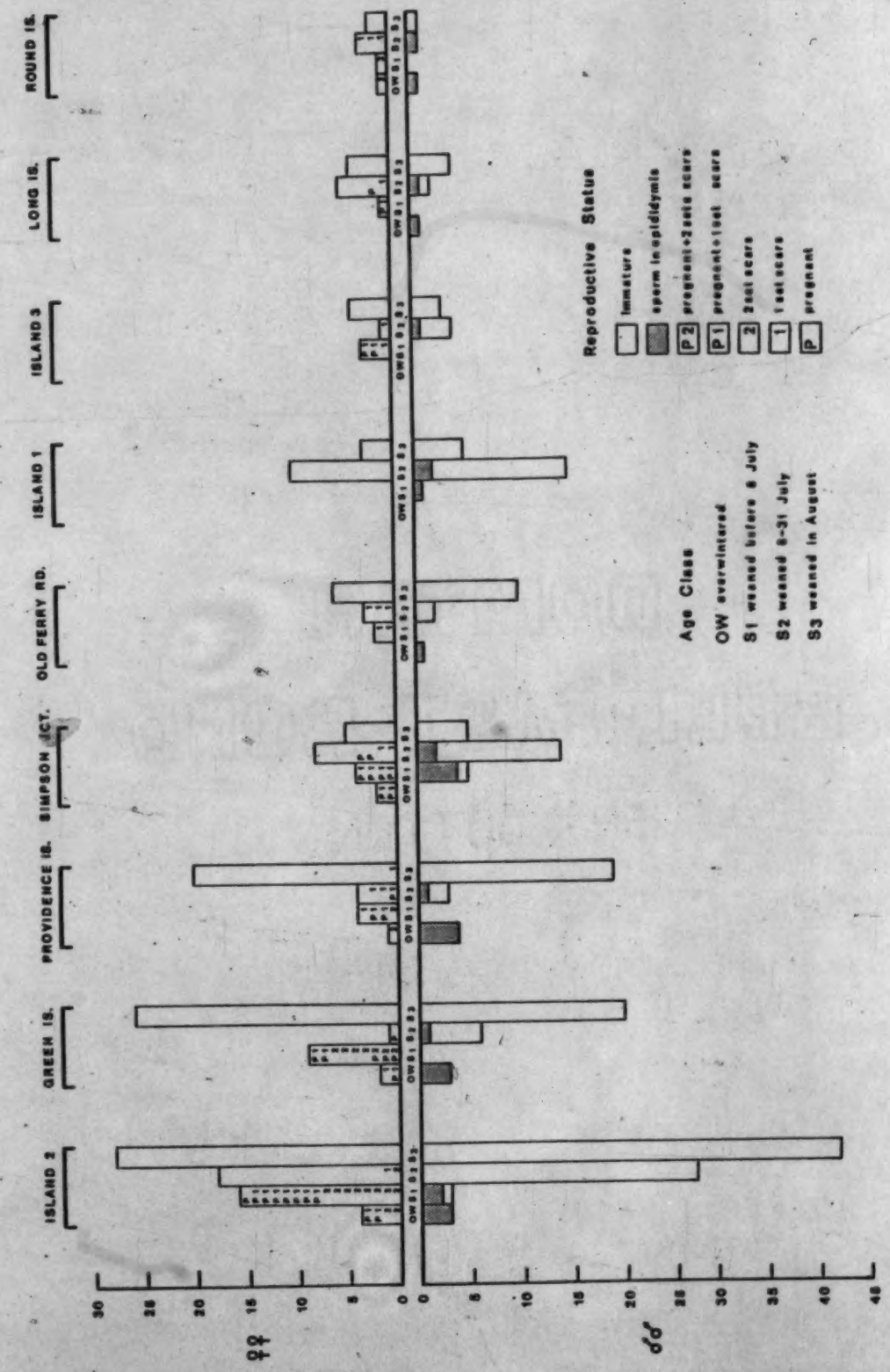

ISLAND 2
GREEN IS.
PROVIDENCE IS.
SIMPSON JCT.
OLD FERRY RD.
ISLAND 1
ISLAND 3
LONG IS.
ROUND IS.
Reproductive Status
Immature
sperm in epididymis
P2 pregnant+2 scars
P1 pregnant+1 scar
2 2 scars
1 1 scars
P pregnant
Age Class
OW overwintered
S1 weaned before 6 July
S2 weaned 6-31 July
S3 weaned in August
♀♀
♂♂

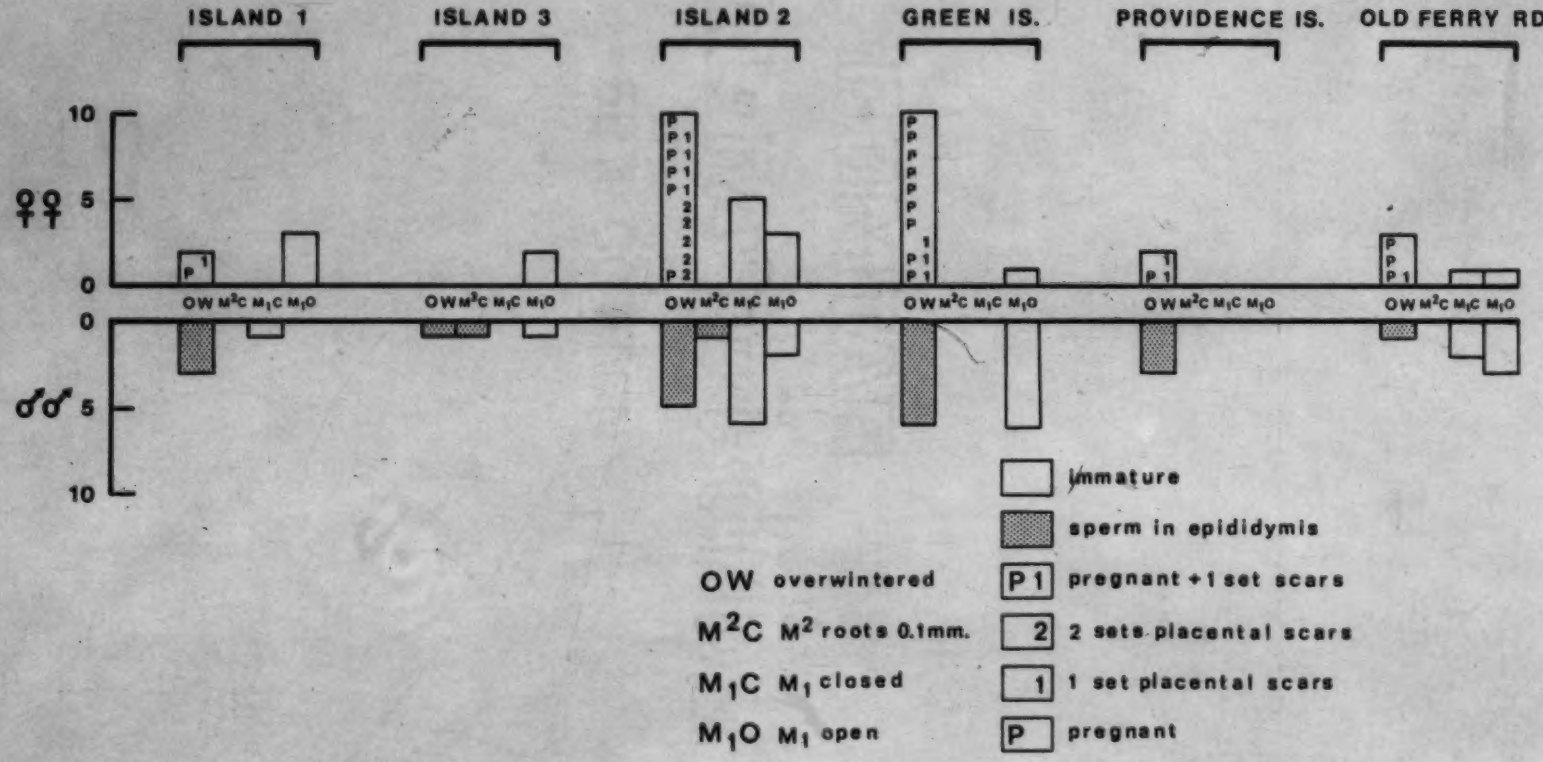
Table 14. Total number and percentage of mature S_2 animals in August in relation to the number of OW animals in June.

	Males			Females		
Populations	(n)	%	OW/S_2	(n)	%	OW/S_2
Island 1	(14)	14.3	0.21	(7)	0.0	0.29
Island 3	(4)	25.0	0.25	(1)	100.0	0.00
Island 2	(27)	0.0	0.19	(18)	11.1	0.56
Green Island	(7)	14.3	0.86	(1)	100.0	10.00
Providence Is.	(4)	25.0	0.75	(4)	75.0	0.50
Old Ferry Road	(2)	0.0	0.50	(3)	100.0	1.00

Table 15. Total number and percentage of mature S_2 animals in August in relation to the number of OW and S_1 animals in August.

Populations	Males			Females		
	(n)	%	$(OW + S_1)/S_2$	(n)	%	$(OW + S_1)/S_2$
Island 1	(14)	14.3	0.07	(7)	0.0	0.00
Round Island	(1)	100.0	1.00	(3)	100.0	0.67
Island 3	(4)	25.0	0.00	(1)	100.0	3.00
Long Island	(2)	50.0	0.50	(5)	40.0	0.20
Island 2	(27)	0.0	0.22	(18)	11.1	1.05
Green Island	(7)	14.3	0.43	(1)	100.0	12.00
Providence Is.	(4)	25.0	1.00	(4)	75.0	1.25
Old Ferry Road	(2)	0.0	0.50	(3)	100.0	0.67
Simpson Jct.	(14)	14.3	0.28	(8)	50.0	0.75

Figure 10 Population structure and reproductive status of *C.rutilus* in June


ISLAND 1
ISLAND 3
ISLAND 2
GREEN IS.
PROVIDENCE IS.
OLD FERRY RD.
10
5
0
0
5
10
♀♀
♂♂
OW M²C M₁C M₁O
immature
sperm in epididymis
OW overwintered
M²C M² roots 0.1mm.
M₁C M₁ closed
M₁O M₁ open
P1 pregnant + 1 set scars
2 2 sets placental scars
1 1 set placental scars
P pregnant

Litter size and number of litters per female

The number of animals per litter, calculated in two ways, is shown for OW and young of the year females in Table 16. No distinction was made between the months during which samples were collected. In both instances OW females had significantly more animals per litter ($P < 0.01$ and $P < 0.001$) than young of the year females. Comparisons for significant difference in litter size between populations can therefore only be made between similar age groups. Among OW females the only samples large enough for statistical comparison were those of Green Island and Island 2. The difference was not significant. Young of the year females at Simpson Junction had significantly smaller litters than those of Providence Island, Green Island, and Old Ferry Road. Young of the year females on Island 2 had significantly smaller litters than those of Old Ferry Road (Table 17). Incidence of resorption of embryos was very low (Table 16).

Frequency of litters is in part related to the onset of the breeding season. In June (Figure 9), one OW female had two clearly distinct sets of placental scars and had one set of implanted embryos which, according to Tupikova (1964), would have been more than ten days from parturition. In August at least two S_1 females had two sets of scars and were pregnant (Figure 9). In one case the embryos were more than ten days, and in the other were six days from parturition. The third female had two sets of scars and a copulation plug in the vagina. All three animals were lactating. Since advanced pregnancy obscures the visibility of placental scars - especially older scars - it is possible that other such females went undetected. However, 44 out of 50 OW and S_1 females had at least two pregnancies by August and two S_2 females

Table 16. Comparison of litter size of OW and young of the year of *C. rutilus* females. Data from all trapping periods are combined.

Embryos only

	Age Class	
	OW	Young of the year
Sample size	25	26
Mean	6.40	5.38
Mean resorption	0.24	0.23
Mean developing ± SE	6.16 ± 0.26	5.15 ± 0.27
Significance		P < 0.01

Developing embryos or new scars

Sample size	38	61
Mean ± SE	6.48 ± 0.23	5.38 ± 0.17
Significance		P < 0.001

Table 17. Comparison of litter size between populations based on developing embryos or new scars. Data from all trapping periods are combined.

	OW		Young of year		
Population	(n)	Mean ± SE	(n)	Mean ± SE	Significance
Island 1	(2)	6.50 ± -	(0)	- ± -	
Island 3	(0)	- ± -	(4)	5.25 ± -	
Long Island	(1)	8.00 ± -	(3)	4.67 ± -	
Round Island	(0)	- ± -	(4)	6.00 ± -	
Island 2	(14)	6.57 ± 0.39	(17)	5.18 ± 0.29	x
Green Island	(12)	6.75 ± 0.28	(12)	5.33 ± 0.47	
Providence Is.	(4)	7.50 ± -	(10)	6.00 ± 0.30	
Old Ferry Rd.	(3)	5.50 ± -	(6)	6.50 ± 0.56	
Simpson Jct.	(2)	4.50 ± -	(8)	4.00 ± 0.27	*
Total	(38)	6.58 ± 0.23	(61)	5.38 ± 0.17	P < 0.001

*Litters of young of the year at Simpson Junction are significantly smaller than those of young of the year on Providence Island (P < .001), Green Island and Old Ferry Road (P < .01).

xLitters of young of the year on Island 2 are significantly smaller than those of young of the year at Old Ferry Road (P < .01).

also had two pregnancies. Although the majority of OW females on Island 2 had bred twice in June, in August they showed evidence of only two pregnancies. It is therefore suggested that for OW and S_1 females two litters are normal, three are exceptional; and that those OW females that produce two litters early in the season do not survive to the end of the season, probably because of the energetic cost of two lactation periods (Migula 1969), one of which may be concurrent with gestation. Increased vulnerability to predation, due to frequent foraging trips away from the burrow while lactating (Herman 1975), may be another reason for non-survival.

The time of cessation of breeding was not determined. No pregnant females were found during the last trapping period (28-30 August) and the only sexually mature male in the sample showed no sign of regression. In much larger samples taken during the third week in August nine pregnant females were taken and there was no indication of testicular regression in sexually mature males.

Body lengths and weights

Except where otherwise stated body lengths and weights are totals of data from all populations and in the case of OW animals data from June, July, and August are combined.

Immature and mature young of the year

No significant differences were found in the body lengths or weights between immature males and females having the same tooth characteristics (Appendix 2). Data from the two sexes were accordingly combined for comparison between age groups. In a previous sub-section

concerned with age classes (Table 8) it was shown that immature animals with M^2 root lengths of 0.1 mm, 0.2 mm and 0.3 mm reached a plateau in body length in August, whereas animals with M_1 open were significantly shorter than those with M_1 closed, which were significantly shorter than those with M^2 roots. A similar relationship occurs in the case of body weight (Table 18).

In addition, immature animals with roots of 0.1 mm, 0.2 mm and 0.3 mm were both shorter and lighter than mature males or mature females of the same M^2 root length (Tables 19 and 20). These results suggest that the reproductive state affects bone growth and weight, but does not affect M^2 root growth. Mature females with M^2 roots of 0.1-0.8 mm also reached a plateau in body length by August which was unaffected by the number of litters produced (Table 21). These results do not support the argument that pregnancies accelerate M^2 root growth. They are in accordance, however with experimentally induced osteosclerosis of the alveolar bone in male and female mice treated with estrogen. Experimental animals showed no changes in either enamel, dentin, cementum or pulp, although they had increased intercellular substance and greater deposition of salts in the alveolar bone in comparison with their litter-mate controls (Stahl *et al.* 1950). Tooth characteristics are therefore considered to be an accurate indication of age of young of the year, from June through August, regardless of reproductive condition.

The weights of the same reproductive females, with M^2 roots of 0.1-0.8 mm, were variable and indicated some increase with age and/or number of litters. Analysis of variance of differences of weights by age was found to be highly significant ($F = 6.38$, $P < .001$). Differences in weights were then tested by Duncan's multiple range test which showed

Table 18. Relationship of body weight (g) to tooth characteristics in non-reproductive animals in August only.

Tooth Character	Mean ± SE	Range	(n)	Significance
M_1 open	11.3 ± 0.44	7.6 - 15.6	(46)	
				P < .001
M_1 closed	15.7 ± 0.38	8.7 - 20.9	(112)	
				P < .001
M^2 root 0.1 mm	17.3 ± 0.14	13.3 - 21.3	(115)	
				ns
M^2 root 0.2 mm	17.4 ± 0.47	14.4 - 20.7	(17)	
				ns
M^2 root 0.3 mm	17.4 ± 0.64	15.5 - 19.0	(7)	

Table 19. Significance of differences between body lengths (mm) of reproductive young of the year females and non-reproductive animals with similar tooth characteristics in August only.

Tooth Character	Status	Mean ± SE	Range	(n)	Significance
M^2 root 0.1 mm	non-reproductive	89.3 ± 0.50	74.0 - 99.0	(115)	P < .001
	reproductive	97.7 ± 2.19	82.0 -104.0	(10)	
M^2 root 0.2 mm	non-reproductive	89.5 ± 1.51	75.0 - 97.0	(17)	P < .05
	reproductive	96.4 ± 2.01	88.0 -102.0	(5)	
M^2 root 0.3 mm	non-reproductive	87.7 ± 2.09	87.0 - 96.0	(7)	P < .001
	reproductive	98.5 ± 1.54	90.0 -103.0	(10)	

Table 20. Significance of differences between body weights (g) of reproductive young of the year females and non-reproductive animals in August only.

Tooth Character	Status	Mean ± SE	Range	(n)	Significance
M^2 root 0.1 mm	non-reproductive	17.3 ± 0.14	13.3 - 21.3	(115)	P < .001
	reproductive	24.2 ± 0.73	19.7 - 27.9	(10)	
M^2 root 0.2 mm	non-reproductive	17.4 ± 0.47	14.4 - 20.7	(17)	P < .001
	reproductive	22.5 ± 0.87	19.1 - 24.3	(6)	
M^2 root 0.3 mm	non-reproductive	17.4 ± 0.64	15.5 - 19.0	(7)	P < .001
	reproductive	25.9 ± 0.87	20.7 - 30.0	(11)	

Table 21. Effect of M^2 root length on mean body length in young of the year females in August, tested by analysis of variance. Number of pregnancies are shown in relation to M^2 root length. P = pregnant and ss = sets of placental scars.

Tooth Character	(n)	Mean length	P+2ss	2ss	P+1ss	1ss	P
M^2 root 0.1 mm	(9)	97.7	-	-	-	6	3
M^2 root 0.2 mm	(6)	95.0	-	1	-	5	-
M^2 root 0.3 mm	(11)	98.4	-	1	7	1	2
M^2 root 0.4 mm	(9)	97.6	-	1	5	3	-
M^2 root 0.5 mm	(11)	95.8	1	6	2	2	-
M^2 root 0.6 mm	(7)	95.4	1	3	3	-	-
M^2 root 0.7 mm	(4)	101.8	-	3	-	1	-
M^2 root 0.8 mm	(2)	95.5	1	-	1	-	-

Mean squares = 25.43

Residual = 41.67

F = 0.61 ns

that in general, body weight increased with increase in M^2 root length (Table 22). There is no obvious explanation for the anomalously heavy weight of females with M^2 roots = 0.3 mm. Analysis of variance of weight by age and pregnancy showed a positive effect of age on weight at a significance of $P < .001$, and an effect of numbers of pregnancies on weight at a significance of $P = .029$. There was no apparent interaction of age and numbers of pregnancies (Table 23). Dewar (1964, 1969) showed that progesterone was responsible for extra-uterine weight gain in laboratory mice, by causing increased water and food intake. He also found that when food was restricted to sub-maintenance levels, progesterone-treated females lost fat, but still gained weight by increased water retention. Weight is therefore a difficult parameter to evaluate when comparing reproductive females. Unfortunately there were relatively few mature young of the year males in samples. Nevertheless, comparisons of mean lengths and weights suggest that such males also attain a plateau in body length, while weights appear to increase with age (Table 24). When divided into equal sample sizes of younger animals (M^2 roots 0.1-0.2 mm) and older animals (M^2 roots 0.3-0.5 mm) the weight difference is significant at $P < .02$. This difference may be accounted for in part by the strong anabolic effect of androgens on muscles (Short 1972).

Mature young of the year and OW animals

OW males were significantly longer ($P < .001$) than young of the year males. However, ranges largely overlapped (Table 25). OW males were also significantly heavier ($P < .001$) than young of the year males, but ranges overlapped only marginally (Table 26). OW females

Table 22. Relationship of body weight (g) to M^2 root length (mm) in young of the year females in August, tested by Duncan's multiple range test. Values underlined are not significantly different at $P < .05$.

n	(6)	(9)	(9)	(11)	(11)	(7)	(2)	(4)
M^2 root length	0.2	0.1	0.4	0.5	0.3	0.6	0.8	0.7
$\bar{X}$ body weight	22.5	24.2	24.4	24.7	25.9	26.6	29.4	30.6

Table 23. Analysis of variance of weight by age and number of pregnancies in young of the year females in August.

Source of variation	Sum of squares	DF	Mean square (variance)	F	Significance of F
Main effects	286.760	11	26.069	5.318	.001
Age	147.224	7	21.032	4.290	.001
Number of pregnancies	59.333	4	14.833	3.026	.029
Age x pregnancies	13.955	9	1.551	0.316	.965
Explained	300.715	20	15.036		
Residual	186.295	38	4.902		

Table 24. Relationship of mean body lengths and weights to M^2 root length in reproductive young of the year males.

M^2 root length	Mean length mm	Mean weight g	(n)
0.1 mm	94.0	19.4	(3)
0.2 mm	94.8	19.7	(5)
0.3 mm	94.8	21.9	(4)
0.4 mm	94.3	21.3	(3)
0.5 mm	92.0	22.7	(1)

				Significance	
	± SE	± SE		length	weight
0.1-0.2 mm	94.5 ± 1.04	19.6 ± 0.57	(8)	ns	$P < .02$
0.3-0.5 mm	94.0 ± 1.59	21.8 ± 0.54	(8)		

Table 25. Significance of differences between body lengths (mm) of OW and young of the year reproductive animals.

	Males			Females			
Age Class	Mean ± SE	Range	(n)	Mean ± SE	Range	(n)	Significance
OW	98.5 ± 0.9	85.0-107.0	(34)	102.3 ± 1.1	92.0-116.0	(39)	P < .01
Young of Year	92.8 ± 0.9	83.0-101.0	(25)	96.6 ± 0.8	81.0-113.0	(69)	P < .01
Significance		P < .001			P < .001		

Table 26. Significance of differences between body weights (g) of OW and young of the year reproductive animals.

	Males			Females			
Age Class	Mean ± SE	Range	(n)	Mean ± SE	Range	(n)	Significance
OW	27.6 ± 0.4	22.6-33.2	(34)	29.7 ± 0.6	23.9-37.5	(39)	$P < .01$
Young of year	20.2 ± 0.4	17.3-24.3	(25)	25.0 ± 0.4	14.5-32.3	(66)	$P < .001$
Significance		$P < .001$			$P < .001$		

were significantly longer and heavier ($P < .001$) than young of the year females, although ranges in both length and weight overlapped broadly (Tables 25 and 26). If two pregnant females, taken in July with no M^2 root, are excluded from the sample, the lowest weight for any reproductive female is 19.1 g. While differences between OW and young of the year animals are highly significant, it is clear that individual animals cannot be classed in late July and August as OW or young of the year on the basis of length in the case of males, and length or weight in the case of females, except at the extremes of ranges.

OW females were also significantly longer and heavier ($P < .01$) than OW males, and young of the year females were significantly longer ($P < .01$) and heavier ($P < .001$) than young of the year males (Tables 25 and 26). With regard especially to range of weights of young of the year males in comparison with OW males and young of the year females, it should be noted that all such young males, with one exception, had M^2 roots of 0.4 mm or less, whereas 24 young females had M^2 roots from 0.5-0.8 mm inclusive.

OW animals in June

Lengths and weights of two populations of OW animals were compared in June. Numbers of OW animals in the four other populations that were sampled in June were too few to allow meaningful comparison. Females on Island 2 were significantly longer ($P < .01$) and heavier ($P < .05$) than Island 2 males. Differences in lengths and weights between OW males and females on Green Island were not significant. Females on Island 2 were also significantly longer ($P < .001$) and heavier ($P < .01$) than females on Green Island. Males on Island 2 were not significantly different in length or weight from males on Green Island (Table 27).

Table 27. Relationship of body length and weight between two populations of OW animals in June.

	Males			Females	
Population	Mean length ± SE	(n)	Significance	Mean length ± SE	(n)
Island 2	97.6 ± 1.33	(5)	P < .01	105.6 ± 1.52	(10)
Significance	ns			P < .001	
Green Island	93.8 ± 1.96	(6)	ns	97.4 ± 1.42	(10)
	Mean weight ± SE			Mean weight ± SE	
Island 2	26.8 ± 1.13	(5)	P < .05	31.0 ± 1.29	(10)
Significance	ns			P < .01	
Green Island	27.4 ± 0.86	(6)	ns	26.8 ± 0.54	(10)

Wounding

Almost all wounding was confined to small punctures along the back and sides of the pelts. Comparison between months shows that wounds were much more frequent in OW females and in immature young of both sexes in June than in August, but that wounding in OW males showed no change with season (Table 28). OW females were also more frequently wounded than OW males in June. Wounding of immature young of the year is clearly correlated with season and inversely correlated with density (Table 28). In August, non-reproductive S_2 animals showed a lower incidence of wounding than S_2 reproductive animals which latter group showed a higher incidence than reproductive S_1 animals (Table 29). These data do not support an inhibition of sexual maturation through fighting.

Incidence of wounding in August shows no consistent correlation with population indices (Table 30). Wounding was infrequent where population indices were high, as for example Island 2 and Island 1. However, incidence of wounding was nil on Island 3 and infrequent on Long and Round Islands where population indices were relatively low. By contrast, incidence of wounding was relatively high at Simpson Junction and Old Ferry Road which had the lowest population indices. The data for Providence and Green Islands are difficult to interpret. On Providence Island, wounding was high for immature males and moderate for immature females. On Green Island, wounding was nil for immature males, but surprisingly high for immature females, since wounding was nil for mature young of the year females. Some of the difficulty in interpretation arises from the necessity of comparing many numerically

Table 28. Seasonal difference in the percentage of *C. rutilus* pelts showing wounds.

Month	Overwintered		Reproductive young of year		Non-reproductive young of year	
	(n)	%	(n)	%	(n)	%
Males						
June	(19)	42.1	(2)	0.0	(19)	36.8
July	(2)	50.0	(9)	33.3	(26)	7.7
Aug.	(13)	46.1	(16)	31.3	(173)	10.4
Females						
June	(27)	66.7	(0)	-	(16)	25.0
July	(2)	0.0	(11)	18.2	(8)	25.0
Aug.	(10)	20.0	(60)	13.4	(127)	11.9

Table 29. Comparison of wounding according to sex, age class, and reproductive status in August.

	Reproductive			
	Males		Females	
Age class	(n)	%	(n)	%
OW	(13)	46.1	(10)	20.0
S_1	(7)	14.3	(40)	2.5
S_2	(9)	44.4	(19)	31.6
S_3	(0)	-	(1)	0.0
	Non-reproductive			
S_2	(65)	10.8	(32)	6.3
S_3	(108)	8.3	(95)	13.7

Table 30. Differences between populations in the percentage of *C. rutilus* pelts showing wounds.

Population	Overwintered		Reproductive young of year		Non-reproductive young of year		Population index
Males	(n)	%	(n)	%	(n)	%	
Round Island	(1)	0.0	(1)	0.0	(1)	0.0	6.0
Island 1	(0)	-	(3)	0.0	(17)	0.0	18.5
Long Island	(1)	100.0	(1)	0.0	(5)	0.0	7.6
Island 3	(0)	-	(1)	0.0	(6)	0.0	8.5
Island 2	(3)	33.3	(2)	0.0	(68)	2.9	22.0
Green Island	(3)	66.7	(1)	100.0	(25)	0.0	16.1
Providence Is.	(4)	50.0	(1)	100.0	(21)	38.1	14.3
Old Ferry Rd.	(1)	0.0	(0)	-	(12)	25.0	4.1
Simpson Jct.	(0)	-	(6)	50.0	(18)	27.8	3.8
Females							
Round Island	(1)	0.0	(4)	50.0	(2)	0.0	6.0
Island 1	(0)	-	(0)	-	(10)	1.0	18.5
Long Island	(0)	-	(3)	0.0	(7)	0.0	7.6
Island 3	(0)	-	(4)	0.0	(4)	0.0	8.5
Island 2	(4)	25.0	(17)	0.0	(46)	2.2	22.0
Green Island	(2)	0.0	(10)	0.0	(25)	32.0	16.1
Providence Is.	(1)	0.0	(9)	11.1	(19)	15.8	14.3
Old Ferry Rd.	(0)	-	(5)	20.0	(6)	16.6	4.1
Simpson Jct.	(2)	50.0	(8)	50.0	(9)	11.1	3.8

small groups, when data must comprise three groups and two sexes for each population. However, the data could support a behavioural difference in tolerance that is independent of density, between small islands and mainland and large islands. Where dispersal is inhibited by a physical barrier, animals may be more tolerant in late summer, than when the possibilities for dispersal with survival are greater. If this is so, it would be in contrast to expectations from some laboratory and penned experiments of crowding (e.g. Friesen 1972), although clearly the latter involve 'islands' which cannot be compared in size or vegetational cover with the small islands in this study.

DISCUSSION

Kreb's effect and island size

The evidence of this study does not support the hypothesis that relative numbers of *C. rutilus* and/or cricetids are negatively correlated with island size. Populations of some adjacent islands differed significantly from each other, but the differences were not necessarily related to the parameter of size. Similarly there was no correlation between island size and instantaneous rate of increase. However, if the populations that were sampled were fluctuating without necessarily being in phase, then peak populations, or mean populations over a period of years might still be negatively correlated with island size. This question might be tested either by sampling a very large number of populations simultaneously, or by long-term studies of a relatively small number of populations.

The evidence does suggest that some island populations of *C. rutilus* are significantly larger than mainland populations. If Long and Round Island data are excluded, the values of all other islands are significantly higher than those of mainland sites (Figure 4). Relatively undisturbed white spruce communities, of easy enough access to be sampled in sequence with islands, were rare within the mainland region. The number of mainland sites that could be sampled was therefore limited and clearly some mainland sites are more favourable than others. However, during the peak year of 1962, a snap-trap index of 26.1 *C. rutilus* was obtained in August from the Old Ferry Road area (Fuller 1969) which was not again even closely approached until the peak year of 1974 (Fuller in press). Compared with mainland indices in August of 4.1 and 3.9 in the present study, it is clear that 1973 was not a peak year, yet Island 2

yielded an August index of 22.0. In addition, during the decline year for *Clethrionomys* of 1968 (Fuller in press) only on islands could appreciable numbers of animals be trapped (Canham 1969).

To what extent snap-trapping in June affected populations in August is a question that cannot be ignored, but neither can it be answered. The rationale for including Round and Long Islands in the August trapping session was based on an awareness that snap-trapping in June might have severely reduced or eliminated the populations of Island 1 and Island 3. That fear proved unfounded. That snap-trapping in June may have reduced the various effects of presence of OW animals on reproduction of the populations of the small islands, remains a possibility. However, Round and Long Islands cannot be considered control populations, since their populations and breeding potential in June is not known. It is possible that removal of some OW and early born animals in June allowed some later born animals to reproduce, that might not otherwise have done so. However, the August samples yielded only one OW animal on Long Island *and* on Island 3, and only two OW animals on Round Island (Figure 9). In addition, Round Island had a larger population of *P. maniculatus* than *C. rutilus*, whereas August samples of Islands 1 and 3 yielded no *P. maniculatus* individuals and Long Island yielded only one such individual.

Tooth growth, body lengths and weights

To the extent that age of many cricetids can only be determined at present by measurements of length and weight, any discussion of changes in such attributes in relation to population fluctuations contains the elements of a circular argument. Clearly, with one summer's data it

is not my intention to discuss population fluctuations, the literature on which is extensive and has recently been reviewed by Krebs and Myers (1974). However, when those authors conclude that median weight *at* sexual maturity differs they only demonstrate that median weight of sexually mature animals differs in different years, which is not the same thing at all.

While most studies of age assignment to *Clethrionomys* have been concerned with root development (Mazak 1963, Pucek and Zejda 1968, Lowe 1971, Zejda 1971 and Viro 1974), the method of Tupikova *et al.* (1968) also included observations before root development. Krebs and Myers (1974) omitted any mention of Tupikova *et al.*, nor did they mention Viitala (1971), who measured increasing crown length, cement layers and neck formation in *C. rufocanus* individuals that were reared in captivity. Unfortunately, Viitala (1971) gave no description of the conditions under which captive animals were maintained, and Lowe (1971) demonstrated that *C. glareolus* individuals that were raised in the laboratory for a long period of time showed abnormal tooth development. Viitala compared rates of M^2 growth in captive animals with that of snap-trapped animals, but again, did not describe his method of determining the age of wild individuals.

In the present study comparisons were made of tooth growth with skeletal growth and weight. Genetic potential for growth, as measured by body length and weight was expressed in young of the year animals, during the study period, through a phase of rapid juvenile growth, which reached a plateau in animals that achieved an M^2 root length of 0.1 mm, and for which the conditions for initiation of sexual maturation were not met. If those conditions were met, the juvenile

growth phase appeared to continue as a second phase of rapid growth with sexual maturation. This phase also reached a plateau in body length, but not in body weight, at least by August.

That body length showed such plateaus is consistent with experimental findings that cartilage responsiveness to growth hormone and somatomedins *in vitro* ceased in rats some time between the age of four and twelve months (Talwar *et al.* 1975). There is no indication that growth hormone and somatomedin production ceases in skeletally mature animals. On the contrary, levels of hormones in serum were monitored during sleep (Weitzman *et al.* 1975) and high levels of growth hormone were found both in boys at puberty and in adult males. Clearly the responsiveness of bone to growth hormone through increasing length is lost in the normal adult. Extrapolation of the results of experiments from man to mouse makes a welcome change. However, if there is a similar loss of responsiveness in *C. rutilus*, which would account for the observed plateaus in body length, it is clearly reversible under whatever conditions initiate sexual maturity in the spring, both in immatures that overwinter and in such reproductive young that may also survive the winter in sexual quiescence.

Fuller (1969 and in press) showed that OW males start growing earlier or more rapidly in spring than OW females. In the present study animals were not sampled until mid June, by which time Island 2 females had surpassed, in length and weight, both Island 2 males and Green Island females. To what extent, if any, genetic differences between the two populations might be involved is not known.

Kalela (1957) observed that *C. rufocanus* females that did not attain maturity in the season of their birth remained at the same weight

during late July and August. Sealander (1966) showed that *C. rutilus* declined in weight in early winter and then remained at a low plateau until early spring. Fuller (in press) observed that skeletal length of *C. gapperi* remained constant during winter, while weight declined and M^2 growth continued. Until March, M^2 root growth averaged approximately 0.005 mm/day. Observations in the present study, while limited to the summer, were in accordance with those of Kalela.

The rationale for comparing tooth growth with bone growth was, as stated, partly based on the mesodermal origin of both bone and dentin. However, the mesoderm that gives rise, in mammalian embryos, to the vertebral column and limb skeleton is not associated with neural crest cells (Balinsky 1965), whereas dentin is derived from the neural crest through induction of ectomesenchyme, which migrates and together with the enamel organ, of ectodermal origin, concentrates in the jaw region (Gaunt *et al.* 1971). Such difference in embryonic origin may therefore partly explain the observed difference in growth response between teeth and axial skeleton. In the mouse embryo, tooth development in the lower jaw was observed to slightly precede that of the upper jaw (Gaunt *et al.* 1971). This developmental difference may explain the closure of the anterior groove of M_1 slightly preceding the closure of that of M^2 which was observed in the present study.

Litter size

Mean litter size in primiparous *Microtus montanus* was, under experimental conditions, significantly greater under long daylength than short daylength (Pinter and Negus 1964). Martinet (1967) also observed that ovulation was quantitatively greater in *M. arvalis* females under

long daylength than in those under short daylength. In the present study OW females bred throughout the season and no attempt was made to distinguish between litter sizes of animals breeding at different daylengths. The significantly higher mean litter size of OW females than of young of the year, which was also observed by Koshkina (1975) and Fuller (in press), is probably in part a function of the larger body size of OW females. Comparision with Martell's data (1975) suggests that in Canada larger litters occur at the higher latitude, which may compensate in part for the lower frequency of litters per female that he found.

In the present study there was no correlation of mean litter size with population size or rate of population growth. This would seem to be in accordance with Krebs' and Myers' (1974) conclusion that litter size is not well correlated with fluctuations of populations. However, Koshkina has recently (1975) shown that in the Salair foothills OW *C. rutilus* females can produce higher mean litters in May, than under longer daylengths in June; that at 54°00' N, mean litter size, in some years, was greater than mean litter size so far recorded for *C. rutilus* at latitudes in Canada north of 60°00'; and furthermore, that mean litter size in May was positively correlated with numbers of OW females. In five different years, when populations contained many OW females, mean litter size in May ranged from 8.04 - 8.66. In three different years, when there were few OW females, mean litter size in May ranged from 6.61 - 7.90. The mean size of 6.61 occurred with the smallest OW spring population of the series, which followed a peak year in 1963. The range of mean litter sizes in the ten years was variable in June, while in July, with the exception of two years (the peak year and the

lowest year, when mean litter size was 5.59 and 6.95 respectively), there was little variation between mean litter sizes (6.03 - 6.61). In some years 7 - 10% of OW females had four litters. Canadian *C.rutilus* are clearly outclassed.

Population structure

There are perhaps four explanations for the striking absence of S_1 males compared to S_1 females on all the islands and one mainland site in August. First, it is possible that the young of first litters were predominantly female. There is no indication in any of the literature on *Clethrionomys* to support this explanation, nor did the results of trapping in June show inequality in the combined juvenile sex ratio. Therefore, this explanation is rejected. Second, it is possible that mortality of young, immature males is higher than that of females. If this is so, then why the relative equality of S_3 males and S_3 females in August? If snap-trapping is a reliable indicator of sex ratio, then sex ratio was equal for juveniles in June and August. If males are more vulnerable than young females to natural predation, then snap-trapping in all months failed to show this. If they are more vulnerable to snap-traps, then trapping in June and August failed to show that. The evidence of this study does not support this explanation.

Third, it is possible that some S_1 males are inhibited from attaining sexual maturation and that such inhibition also involves suppression of M^2 root growth. If the slight total surplus of S_2 males in August is subtracted from that class and added to the S_1 class it only results in eight additional males which increases the percentage of S_1 males only to 35.4. Certainly the mainland site of Simpson Junction

with an equal sex ratio of S_1 animals had no OW males in the samples in August. However, neither did Island 1 nor Island 3, and Old Ferry Road, Long Island and Round Island only had one OW male, and yet in three of the latter four populations no S_1 males were present. This, in spite of the fact that in those populations some S_2 males were mature. On Island 1 one S_1 male was present and two S_2 males were mature. In order to support this third possible explanation such anomalies have to be considered as well as a hormonal explanation for inhibition of M^2 growth in some animals but not in others. If such an explanation is tenable, the evidence to support it would be very complex and in the circumstances it must be rejected.

Fourth, it is possible that mortality of young *mature* males may be higher than that of similar females, early in the breeding season. Due to high production of androgens and possible intolerance by OW males, young mature males may not only be inclined to wander far, but are given a certain amount of incentive to do so, and therefore may be subject to higher predation due to greater exposure. On the mainland and large islands this would lead to dispersal and colonization, as described by Anderson (1970) and, in this connection, Simpson Junction could be a colonizing site. On the islands there is the barrier of the river and while it may inhibit, it may not prevent, dispersal by swimming. In Finland marked voles were found to move between islands (pers. comm. Fuller), although the distances are not known. In the Mackenzie River, the stomachs of a sample of northern pike, gill-netted in summer, were found to contain 60% by volume of small mammals (Hatfield *et al.* 1972). While dispersal by swimming may offer limited chances of survival, it may, to some, be an attractive alternative to staying. The second

observation that supports this explanation is the highly significant difference in mean weight of S_1 males compared with that of both S_1 females and OW males. The range of weights of S_1 males does not even overlap with that of OW males, whereas that of S_1 females overlaps broadly with that of OW females. Since weight was shown to be, in large measure, a function of age in S_1 females and small samples indicate that this is also true for S_1 males, such a weight gap, in what would be expected to be a continuum, is further evidence that this class of older S_1 males had disappeared from all sampled populations except that of Simpson Junction.

If this fairly simple explanation is true it contains possibilities for genetic change. If early-born S_1 females do not breed with littermates, or among their own cohort, but breed instead with OW males (probably their fathers) a class of young could be produced with a high frequency of certain alleles. Such a class might vary in size and therefore in influence in different years. Frequency of certain alleles might then be a function of population structure. However, this is no more than speculation.

Seasonal differences in behaviour

If it is argued that young, sexually mature males disperse and to a large extent fail to survive early in the breeding season, there must be sexually different behaviour and seasonally different behaviour if intolerance is part of the reason for dispersal. Wounding is an unsatisfactory measurement of intolerance, since from examination of pelts alone it is not possible to tell who is biting whom. That a high percentage of OW females exhibited frequent small bites may indicate intra-sexual strife, or it may only be an indication of male aggression

during copulation, or attempts at copulation. Zirul (1968) observed this phenomenon in red squirrels. Maclean (1970) described a neurological basis for biting and mouthing during sexual behaviour in cats, which he extrapolated to human behaviour. Severe wounding of females that were approaching sexual maturation, by males that were already mature, was observed in laboratory caged pairs of *Clethrionomys* (unpublished data). In such instances the females were unable to escape.

It seems reasonable to postulate that rapidly maturing young females are ambivalent in their reactions to mature males and while perhaps not ready to copulate, can temporarily escape and are not necessarily driven to disperse. Wounding in this study was not severe and never approached the level described by Koshkina (1965), when young of the year were apparently inhibited from maturing by aggression of OW animals. While Koshkina aged snap-trapped animals by characteristics of M^2 growth, she did not use this information in her paper to distinguish between early and late born young of the year, which makes her data difficult to interpret. She also documented population indices which were extremely high for *Clethrionomys* by northern standards. Bujalska (1970) discussed maturation of *C. glareolus* females at densities of up to 100 animals/ha on a 4 ha island and never mentioned wounding in her paper. The obvious inference is that if it occurred it was too slight to be noted in live animals.

There is very little evidence in the literature to support the theory of inhibition of maturation through a pituitary-adrenal stress mechanism (Christian and Davis 1964), except under pathological conditions of laboratory crowding. In his study of *Microtus pennsylvanicus* (1971), Christian concluded that growth and reproduction of young males and

females were inhibited by changes in aggressive behaviour with changes in density. Aggression was measured by presence and degree of wounding on pelts. He observed that fighting and wounding was limited almost entirely to sexually mature males in both years of the study. Nevertheless, he concluded that immature males and females were inhibited from maturing and from growing. The connection between adult aggression and juvenile inhibition was not demonstrated. One is left to infer that the spectator sport of watching adult males fighting constituted such stress for juveniles that growth ceased and maturation was prevented. It is to be noted that autopsies did not include examination of adrenal glands. In addition, the sample sizes of females that were presented to show reproductive status between years, were too small to reach any but the most tentative conclusions.

A hypothesis of stress induced inhibition of maturation is not *per se* debated here, but rather the evidence that Christian has presented to support his proposed mechanism of inhibition. Physiological and behavioural changes may be induced by social interactions that do not necessarily involve adrenal function or secretion of adrenocorticotrophic hormone (ACTH). The interaction and facilitation of hormones; environmental effects; and changing sensitivity of target organs makes the physiological process of maturation and reproduction exceedingly complex. Pheromones, for example, have been shown experimentally to inhibit maturation of young female mice (*Mus*), to accelerate maturation, to synchronize estrus and to induce termination of early pregnancy. In addition they also may form a system of communication by which individuals and strangers can be identified and social and reproductive status and territories indicated (Bronson 1971, Eisenberg and Kleiman 1972).

Stress may or may not be involved in such interactions or if it occurs, it may only be at a low level. Unfortunately, some of the necessary circumstances are difficult to envisage in natural conditions. For example, urine from virgin female mice delayed sexual maturation of immature females, while adult male urine accelerated sexual maturation (Cowley and Wise 1972). Unless there is a severe shortage of mature males, it seems unlikely that weaned immature females would not in the normal course of events be exposed to urine of such males. However, although such mechanisms need to be confirmed under natural conditions, they would seem to suggest a far more energetically economical means of social regulation then the stress and strife that Christian envisaged.

Maturation of young of the year

It is rare, but not unknown for late-born *C. rutilus* females to mature in the same season. Normally, according to the authors cited in the Introduction, late litters of *Clethrionomys* remain immature and the survivors form the next season's breeding stock. Anderson (1970) discussed this phenomenon and that of dispersal of early-born animals with respect to gene flow. The question that is usually asked is: Why does the percentage of early-born animals attaining maturity within the same breeding season vary from year to year? The question that should have equal weight is: Why do the late-born not mature regardless of variations in densities of populations?

It is unlikely that temperature can have any effect on failure to mature since at 61°00' N August can be as warm as, or warmer than, June and night frosts can occur in both months. The quality of food could be a factor in terms of new green growth. Day (1968) gave the mean drouth

point, when plant growth and evaporation have exhausted the available soil moisture, and growth rates are reduced, as 22 June at Fort Providence. The beginning of the growing season was given as 9 May. Pinter and Negus (1965), Pinter (1968) and Martinet and Meunier (1969) showed that new green growth stimulates maturation and reproduction of *Microtus* spp., especially when combined with long daylength. Further experiments by Negus (quoted from personal communication by Reiter and Sorrentino [1971]) showed that green plant food resulted in smaller pineal glands, regardless of daylength. The presence of green plant material in stomach samples obtained by Dyke (1971) coincided with the duration of breeding season in *C. gapperi* at Heart Lake, N.W.T.. There is no experimental evidence to show whether new green growth has any affect on maturation of *C. rutilus* or *C. gapperi* but until it is tested it remains a possibility.

Evernden and Fuller (1972) showed that maturation of *C. gapperi* laboratory females was stimulated by white and blue radiation and increased daylength in late winter. They also found that the altered properties of melting snow in late spring allowed penetration of short wave lengths. Once maturation is attained, estrous cycles continue for a certain length of time and normally result in reproduction in spite of the fact that daylength may be decreasing. To what extent the rhythm is endogenous or is dependent on a minimum daylength is not known. In the case of *C. rutilus* in the Fort Providence area, pregnant females were observed in mid to late August, over three years, and males were sexually active until late August (Fuller 1969).

The evidence of this study supports the first two premises of my second hypothesis, but not the third premise. The hypothesis was

based on the assumption that there is a threshold of sensitivity to decreasing daylength, below which any young that are weaned are unlikely to mature, and that maturation becomes less likely the further below the threshold that they fall. Young that are weaned slightly below the threshold might mature if other conditions are favourable, but not if they are inhibiting. Other factors are not therefore excluded, only their relative weighting is changed. Evidence to support the existence of such a threshold was recently presented by Hoffman and Cullen (1976). They found that when female rats were exposed to different photoperiods, animals showed an increased sensitivity under short photoperiods to the inhibitory feed-back effect of estrogen, which resulted in low serum levels of luteinizing hormone (LH). These results are in accordance with Short's (1972) statement that 'The most generally accepted explanation for the phenomenon of puberty is that it represents a progressive *loss* of hypothalamic sensitivity to the inhibitory effects of steroidal feedback'.

Fraschini *et al.* (1971) found that injection of two pineal compounds selectively inhibited secretion of follicle stimulating hormone (FSH) and LH, causing delayed puberty in immature rats. Evidence was also obtained that the compounds exerted their effects on receptors in the hypothalamus and midbrain, which were sensitive to those compounds. If the receptors that are sensitive to one of the pineal compounds (melatonin) are also involved in a sensitivity to estrogen, then an increase in melatonin might lower the threshold of sensitivity to the negative effect of estrogen on LH secretion in juveniles. Increase in the rate of formation of melatonin in darkness was obtained experimentally by Axelrod (1975). Axelrod also observed circadian rhythms in

biosynthesis of some pineal compounds (1971, 1975) and described the reception and transmission of light to the mammalian pineal (1970).

Based on reproductive data in relationship to age and times of trapping, the threshold of sensitivity for young animals appeared to fall within the last three weeks of July. An approximately similar time can be inferred from data presented by Schwarz *et al.* (1964). During this time at 61°00' N, daylength was decreasing from 18.75 hours to 17.00 hours. At the time of the summer solstice at 61°00' N daylength is 19.25 hours, with the remaining 4.75 hours being twilight. After the solstice, daylength, at first almost imperceptibly, then more rapidly, decreases, until by the end of August it has reached 14.25 hours. If such a threshold of sensitivity is accepted, then it follows that, given equally good litter survival, OW females that breed early will produce a greater number of S_1 young, because of a greater time span in which to produce two litters before the end of June, which, in turn, allows weaning to be completed in early July. An equal number of OW females starting to breed later will produce fewer S_1 young and their second litters may be S_2 or S_3 animals. Since S_1 young normally produce the greater part of the S_3 class, such a difference in timing of breeding (given the same number of OW females) can make the difference between a large, late summer population and a small one.

It is proposed that this difference in breeding potential alone could account for the difference in indices of population on Island 2 (27.0) and Green Island (14.0) as extrapolated or interpolated for mid August or, if preferred, for the unadjusted indices of 22.0 and 15.9 respectively. It could also account for the differences in instantaneous rates of increase of 0.48 young/female/day for Island 2

and 0.36 young/female/day for Green Island. In addition, since first litter S_1 females (M_1 closed) were approaching estrus on Island 2 in the third week of June, S_1 animals could have produced late S_2 animals which might account, in part, for the large number of S_2 young on Island 2 in August.

Clearly a high number of OW females breeding in mid, or late May can produce as many or more S_1 animals as a small number of OW females breeding in late April, so that early breeding is not a necessary condition , but it is a sufficient condition for producing large summer populations. Survival of young is naturally a critical factor. Nevertheless, since there are so many variables to consider in the question of reproduction it is important first to attempt to establish physiological potentials, as Leopold (1933) demonstrated by his comparison of intrinsic rates of increase in different species.

Nine of ten OW females taken in June on Island 2 had, or would have, produced two litters by the end of June (i.e. two litters of S_1 young). The OW females on Green Island could only have produced S_2 or in most cases S_3 young, if they had conceived second litters at post partum estrus. In the August sample from Green Island very few S_2 animals were present. It is apparent that while the samples from Island 2 (at 7 ha) can reasonably be considered representative of the population (if one ignores the argument of differences in trappability), the June sample from Green Island (at 30 ha) may not have been representative of the whole. Clearly, from the August samples, a somewhat higher number of S_1 females must have been present in June (and missed in the small late July sample) in order to have achieved the age and produced the

number of litters that they did. However, I do not consider that these few exceptions are sufficient to disprove the rationale that is presented to account for the differences between the two populations. Unfortunately, the June samples from other populations are insufficient to permit similar comparisons to be made.

Maturation of young in relation to other studies

The absence of evidence to support an inhibition of maturation of S_2 animals by OW and S_1 animals in this study is clearly in contrast with conclusions reached by such researchers as Koshkina (1965) and Martell (1975) working with *C. rutilus*; Kalela (1957), working with *C. rufocanus*; and numerous authors working with *C. glareolus*. The latter species is found at lower latitudes, has a longer breeding season, with winter breeding occurring not uncommonly, and appears to attain much higher densities than occur, for the most part, in northern populations of *C. rutilus*. For these reasons studies of *C. glareolus* will not be considered here. However, in passing, I should like to note that Bujalska (1970), working with live animals on a 4 ha island, observed, in a peak year, a summer population of 400 marked animals. She also made the important observation that while the numbers of OW females varied in each of the three springs of the study period and the summer population also varied between years, the number of mature females remained constant each summer, although clearly the percentage of juveniles attaining maturity varied considerably. The fact that the numbers remained constant indicated to Bujalska that the number of suitable territories (with associated social interactions) limited the female breeding base. If she had used percentages instead of numbers then she would have concluded

that maturation of young females was inversely proportional to the number of OW females in spring; and that such density dependence was a causal relationship, instead of an arithmetical one.

Discussion of conclusions reached by different authors, even when restricted to the same species, is usually hampered by the difficulty in comparing published data, when the basic raw data are unavailable and the parameters used in grouping data in one study may not be the same as those of another study. Here, it is only possible to conclude that Koshkina (1965, 1974a, 1974b) appeared to have good evidence for adult inhibition of maturation of young in her long term study, the complete version of which (1974a) has yet to be translated into English (and therefore, regrettably, is unavailable to me). Nevertheless, a figure showing 0.0% maturation of young with high densities of OW animals is hard to debate, since zero is an absolute. However, Koshkina was working at lower latitudes in the Salair and obtained much higher indices of populations than has been observed in the general area of the present study and different regulating mechanisms may operate under such densities.

I will however, debate Martell's (1975) conclusion that, in northern taiga, the percentage of first litter young breeding in the year of their birth appeared to be inversely related to population density in early summer. Pertinent data from Martell (1975) are summarized in Table 31. The early spring taiga population indices were 4.4, 1.9, and 1.4 for 1971, 1972 and 1973 respectively. No young were trapped in any year in mid July with closed M^2 grooves. When trapping periods for mid July are compared it is seen that in 1971, 23.7% of 59 young were mature; in 1972, 0.0% of 49 young were mature; and in 1973, 14.3% of 14

Table 31 Reproductive data in relation to taiga population indices and M^2 characteristics. After Martell (1975; Table 4, Figure 4 and Appendix 1).

Year	Trapping period	Number of TN	(n)	M^2 open % reproductive	(n)	M^2 closed % reproductive	(n)	neck formed % reproductive	(n)	roots % reproductive
1971	July 14	1,014	(59)	23.7	(0)	-	(0)	-	(0)	-
	July 28	300	(13)	15.4	(3)	33.3	(0)	-	(0)	-
	Aug. 28	2,182	(152)	0.0	(13)	7.7	(16)	12.5	(3)	100.0
1972	July 18	3,000	(49)	0.0	(0)	-	(0)	-	(0)	-
	Aug. 10	3,000	(53)	3.8	(18)	5.6	(3)	67.7	(1)	100.0
	Sept. 1	2,460	(80)	0.0	(13)	15.4	(4)	75.0	(4)	100.0
1973	July 11	2,400	(14)	14.3	(0)	-	(0)	-	(0)	-
	Aug. 4	3,300	(16)	18.8	(11)	63.6	(8)	100.0	(2)	100.0
	Aug. 22	3,000	(34)	0.0	(1)	0.0	(4)	66.7	(6)	100.0

Year	June OW catch/100 TN	Beginning of breeding season	Spring critical period
1971	4.4	1 - 30 June	most favourable
1972	1.9	10 June - 10 July	least favourable
1973	1.4	1 - 30 June	intermediate

young were mature. These data do not support density dependent inhibition of early-born young. At least for 1971 and 1972 the reverse is the case. In the late July - early August trapping period, 33.3% of early-born young (as determined by closed grooves and neck) matured in 1971. In 1972, 15.0% matured and in 1973, 80% matured. It must be pointed out that only 3 animals were trapped in this period in 1971, compared with 21 in 1972 and 19 in 1973. However, there were only 300 trap nights in 1971, compared with 3,000 in 1972 and 3,300 in 1973. While such discrepancies are often unavoidable under field conditions, the magnitude of the difference introduces a strong bias in the 1971 catch. In each year all young with roots were mature by August, although sample sizes are necessarily small. No young with M^2 open matured in late August in any year, regardless of different August densities.

Onset of breeding was relatively early in 1971 and 1973 and therefore positively correlated with maturation of early-born young in those years. In 1972, it was delayed about ten days, and no early-born young had matured by mid July and only 14.3% by early August. Onset of breeding was, therefore, negatively correlated with maturation of early-born young in that year. The Spring Critical Period was most favourable in 1971, less favourable in 1973 and least favourable in 1972, which seems to suggest a causal connection between favourable spring conditions, early initiation of breeding and maturation of early-born young. Martell (1975, Figure 4) also observed that recruitment was high in 1971 and 1973 and lowest in 1972, which presents difficulties for the theory of homeostasis, attractive though such a theory may be.

That data may honestly be interpreted in different ways due to different implicit assumptions or explicit biases on the part of

researchers was demonstrated by Kreb's interpretation of data on lemmings (1974) and Fuller's re-interpretation of the same data, which resulted in very different conclusions (Fuller 1967). Martell made the assumption that M^2 grooves closed at an earlier chronological age in mature animals, but gave no evidence in his thesis to support that assumption. Nor have I been able to find any supporting evidence in any of the literature, except for Viitala's statement (1971) that the M^2 of mature, wild female *C. rufocanus* showed a faster rate of growth than mature males and immature males and females. Martell grouped males and females together. The inter-sex difference in development of M^2 (Tables 9 and 10) serves to confuse the issue further. The whole question of growth and differentiation of M^2 in *Clethrionomys* is in need of additional study under as near natural conditions as possible.

It may be argued that a theory of a threshold of light sensitivity affecting maturation of young could not apply at a latitude of 68°00' N. At that latitude the sun first sets on 19 July. However, shortening photoperiod may be at least as, or more important than absolute daylength. Lecyk (1963) showed that 10-day old *Microtus arvalis* were inhibited from maturing when placed on a gradually decreasing light regime starting on 10 May. In northern regions another associated factor may be that of change in angle of the sun, which alters the quality of radiation by changing the ratio of short to long wavelengths. Change in light when accompanied by change in quality of food, or temperature may also have an additive, or synergistic effect. It may be argued that such a short period of time can hardly make the difference between breeding and not breeding. But the North has an imperative of its own and many authors have shown that timing of reproduction in

widely divergent northern species is critical and has a very narrow safety margin.

Another question that is raised is whether high numbers of immature young can inhibit maturation of other immature young under natural, wild conditions. Relative numbers of S_2 animals were high on Island 1 and Island 2, which may have constituted an unfavourable condition for maturation. However, one of the most interesting questions that arises from this study is why breeding should apparently start earlier in one population (Island 2) than another in the same region (Green Island), in the same year? Spring was relatively early in 1973, with early snowmelt on the mainland and early break-up of river ice. It is possible that breeding started at the same time on both islands, but that early pregnant females did not survive on Green Island, perhaps due to unfavourable snowmelt conditions. Or spring critical periods may have differed on the two islands. Evernden (pers. comm.) hypothesized that small islands, being more influenced by ice conditions, may have a more stable spring critical period than larger islands. Whatever the reasons (and they could include differences in food, fall populations and overwintering habitat) it would be interesting to know if such a difference occurs in other years.

Significance of results

That the evidence of this study does not support the hypothesis that relative numbers of *C. rutilus* and/or cricetids are negatively correlated with island size does not mean that such a relationship might not exist over time; or might not exist more consistently in coastal

islands, or in more temperate regions, or with communities of other cricetid species. My conclusion only demonstrates that if such a relationship exists, it was not evident within the limits of time and location to which this study was restricted, nor for the cricetid species that occurred in the areas that were sampled.

That the barrier of a great river to dispersal of young *C. rutilus* in summer is more effective than barriers of muskeg and sparse ground cover on the mainland was to be expected. That the river barrier may not be completely effective would not have been suspected from the evidence of this study, if my only criterion for age had been weight or length. That S_1 males were not present in island populations in August in approximately the same ratio as S_1 females was only apparent from the data that were accumulated on tooth development in relation to growth and maturation. Without such evidence I would probably have assumed that some of the young present were S_1 males and that they were socially inhibited from maturing. The conclusion that mature S_1 males dispersed, rather than died, may be debated, since from this study I only obtained the negative evidence of their absence. However, this conclusion may be tested by further sampling, by tracing marked animals, by sampling the stomach contents of pike, or by design of experimental studies.

Dispersal is only one component of population dynamics. Reproductive potential is the corner stone on which the rise and fall of populations must rest. In their investigation of physical differences that characterize seasonal generations of many small rodents, Schwarz *et al.* (1964) obtained experimental results which showed that reduced daylength was the cause of failure to attain maturation in late summer generations of *Lagurus lagurus* and tundra populations of *Microtus gregalis*

major. Recent neurological evidence for pineal-mediated effects of daylength on sexual maturation and gonadal function provides the necessary association between the abiotic phenomenon of daylength and the physiological phenomenon of maturation. Clearly, if an animal is physiologically incapable of maturation at a given time it cannot be inhibited by mature animals. It is therefore important to distinguish between those young that for a non-social environmental reason are physiologically capable of maturation, those that are not, and those that are perhaps on the borderline. Since, in many studies, young are frequently collected in late summer, it is necessary to be able to age such animals with a fair degree of precision if conclusions made about maturation and reproduction are to be valid. In many studies of population fluctuations it is not easy to distinguish between cause and effect, particularly in the case of attributes associated with increasing, declining and peak populations.

The results of this study have raised more questions than they have answered. It is hoped that the questions are worth asking and will lead to greater understanding. In the wealth of literature dealing with microtine population fluctuations and accompanying reproductive variations, much emphasis has been placed on social interactions and, with the exception of food, relatively little on the effect that other biotic and abiotic factors can have on the physiology and behaviour of individuals. Even territory is considered mainly in terms of a negative social relationship, rather than a positive non-social relationship. The reason for this is not hard to find. As a species we have become relatively insensitive to the abiotic and exceedingly sensitive to the social context. Even as biologists our biases are clear. Not that this

is undesirable, as long as we recognise them. Science is advanced by a democratic process in which a diversity of ideas are represented and given expression. The kind of questions we ask are an expression of our biases. But an awareness of that fact is, as Socrates well knew, the *sine qua non* for objectivity.

LITERATURE CITED

Anderson, P.K. 1970. Ecological structure and gene flow in small mammals. Symp. Zool. Soc. 26:299-325.

Axelrod, [illegible]. 1970. The pineal gland. Endeavour 29:144-148.

_____ 1971. Neural control of indoleamine metabolism in the pineal. Pages 35-47 *in* G.E.W. Wolstenholme and J. Knight. The Pineal Gland. A Ciba Foundation Symposium. Churchill Livingstone. Edinburgh. 401 pp.

_____ 1975. Relationship between catecholamines and other hormones. Pages 1-27 *in* R.O. Greep. Recent Progress in Hormone Research. Proc. 1974 Laurentian Hormone Conference. Vol. 31 Academic Press. New York. 631 pp.

Balinsky, B.I. 1965. An Introduction to Embryology. W.B. Saunders Co. Philadelphia, Second edition. 673 pp.

Brambell, F.W.R., and I.W. Rowlands. 1936. Reproduction of the bank vole (*Evotomys glareolus*, Schreber). Phil. Trans. R. Soc. (B):71-120.

Bronson, F.H. 1971. Rodent pheromones. Biol. Reprod. 4:344-357.

Bujalska, G. 1970. Reproduction stabilizing elements in an island population of *Clethrionomys glareolus* (Schreber, 1780). Acta Theriol. 15:381-412.

Canham, R.P. 1969. Serum protein variation and selection in fluctuating populations of cricetid rodents. Ph.D. Thesis. Dept. Zool. Univ. Alta. 121 pp.

Christian, J.J. 1971. Fighting, maturity and population density in *Microtus pennsylvanicus*. J. Mamm. 52:556-567.

Christian, J.J. and D.E. Davis. 1964. Endocrines, behavior, and population. Science, N.Y. 146:1550-1560.

Cowley, J.J. and D.R. Wise. 1972. Some effects of mouse urine on neonatal growth and reproduction. Anim. Behav. 20:499-506.

Day, J.H. 1968. Soils of the upper Mackenzie River area Northwest Territories. Research Branch, Canada Dept. of Agriculture. 77 pp.

Dewar, A.D. 1964. The nature of weight gain induced by progesterone in mice. Q.J. Expm. Physiol. 49:151.

_____ 1969. The mechanism and nature of extra-uterine weight gain of pregnancy in the mouse. J. Reprod. Fert. Supplement. 9:17-26.

Dyke, G.R. 1971. Food and cover of fluctuating populations of northern cricetids. Ph.D. Thesis. Dept. Zool., Univ. Alta. 245 pp.

Eisenberg, J.F., and D.G. Kleiman. 1972. Olfactory communication in mammals. Ann. Rev. Ecol. and Syst. 3:1-32.

Evernden, L.N., and W.A. Fuller. 1972. Light alteration caused by snow and its importance to subnivean rodents. Can. J. Zool. 50:1023-1032.

Fedyk, A. 1974. Growth and body composition in post-natal development of the bank vole. II Differentiation of seasonal generations. Acta Theriol. 19:403-427.

Fraschini, F., R. Collu and L. Martini. 1971. Mechanisms of inhibitory action of pineal principles in gonadotropin secretion. Pages 259-273 *in* G.E.W. Wolstenholme and J. Knight. The Pineal Gland. A Ciba Foundation Symposium. Churchill Livingstone. Edinburgh. (1975).

Friesen, J. 1972. Spatial and temporal utilization of semi-natural enclosures by *Clethrionomys gapperi*, *Clethrionomys rutilus* and *Peromyscus maniculatus*. M.Sc. Thesis. Dept. Zool. Univ. Alta. 91 pp.

Fuller, W.A. 1967. Ecologie hivernale des lemmings et fluctuations de leurs populations. La Terre et la Vie. 21:97-115.

_____ 1969. Changes in numbers of three species of small rodent near Great Slave Lake, N.W.T., Canada, 1964-1967, and their significance for general population theory. Ann. Zool. Fennici 6:113-144.

_____ (in press) Demography of a subarctic population of *Clethrionomys gapperi*: Size and Growth.

Gaunt, W.A., J.W. Osborn and A.R. Ten Cate. 1971. Advanced Dental Histology. John Wright and Sons Ltd., Bristol, England. 129 pp.

Gebczynski, M. 1975. Heat economy and the energy cost of growth in the bank vole during the first month of postnatal life. Acta Theriol. 20:379-434.

Gorbman, A., and H.A. Bern. 1962. A textbook of comparative endocrinology. John Wiley and Sons Inc., New York. 468 pp.

Hatfield, C.T., J.N. Stein, M.R. Falk, C.S. Jessop and D.N. Shepherd. 1972. Fish resources of the Mackenzie River valley. Interim Report I. Vol. II. p. 289. Environmental-Social Committee, Northern Pipelines, Task Force on Oil Development.

Herman, T. 1975. Patterns of activity of subarctic voles. M.Sc. Thesis. Dept. Zool., Univ. Alta. 40 pp.

Hoffman, J.C. and A.M. Cullin. 1976. Effect of photoperiod length on luteinizing hormone levels in estradiol-treated ovariectomized rats. Fed. Proc. (Abstr.) 2258 March.

Kalela, O. 1957. Regulation of reproductive rate in subarctic populations of the vole, *Clethrionomys rufocanus* (Sund). Ann. Acad. Sci. Fennici, Ser. A, IV Biologica, No. 34. 60 pp.

Koshkina, T.V. 1965. Population density and its importance in regulating the abundance of the red vole. Bull. Moscow Soc. Natur., Biol. Sect. 70(1):5-19. (English Transl.)

_____ 1974a. Population regulation of numbers in rodents. Avtoreferat. (Dissertation for degree of doctor of biological sciences.) Sverdlovsk. 59 pp. (in Russian).

_____ 1974b. Population control in voles of genus *Clethrionomys*. Trans. First Int. Theriol. Congr., 1:296-297. (Abstr.)

_____ 1975. Regulative adaptations in populations of the red vole (*Clethrionomys rutilus*) under optimum conditions of its range. Fauna and Ecology of Rodents. 12:5-61 (in Russian).

Krebs, C.J. 1964. The lemming cycle at Baker Lake, Northwest Territories, during 1959-1962. Arctic Inst. N. Amer. Tech. Paper No. 15. 104 pp.

Krebs, C.J., M.S. Gaines, B.L. Keller, J.H. Myers, and R.H. Tamarin. 1973. Population cycles in small rodents. Science 179:35-41.

Krebs, C.J., and J.H. Myers. 1974. Population cycles in small mammals. Advances in Ecol. Res. 8:267-399.

Lecyk, M. 1963. The effect of short daylength on sexual maturation in young individuals of the vole *Microtus arvalis* Pall. Zool. Pol. 13:77-86.

Leopold, A. 1933. Game management. Charles Scribner's Sons, New York. 481 pp.

Lowe, V.P.W. 1971. Root development of molar teeth in the bank vole (*Clethrionomys glareolus*). J. Anim. Ecol. 40:49-61.

MacArthur, R.H. 1972. Geographical Ecology. Harper and Row Publishers Inc., New York. 269 pp.

MacLean, P.D. 1970. The limbic brain in relation to the psychoses. Pages 129-146 *in* P. Black. Physiological correlates of emotion. Academic Press New York. 309 pp.

Martell, A.M. 1975. Demography of tundra and taiga populations of *Clethrionomys rutilus*. Ph.D. Thesis. Dept. Zool., Univ. Alta. 170 pp.

Martinet, L. 1967. Cycle saisonnier de reproduction du campagnol des champs *Microtus arvalis*. Ann. Biol. Anim. Biochim. Biophys. 7: 245-259.

Martinet, L., and M.Meunier. 1969. Effect of the seasonal change in lucern feed on growth, mortality and sexual maturation of the field vole *Microtus arvalis*. Ann. Biol. Anim. Biochim. Biophys. 9:451-462.

Mazak, V. 1963. Notes on the dentition in *Clethrionomys glareolus*, Schreber, in the course of post natal life. Säugtier. Mitt. 11:1-17.

Migula, P. 1969. Bio-energetics of pregnancy and lactation in the European common vole. Acta. Theriol. 14:167-179.

Morrison, P.R., F.A. Ryser and R.L. Strecker. 1954. Growth and the development of temperature regulation in the tundra red-backed vole. J. Mammal. 35:376-386.

Pinter, A.J. 1968. Effects of diet and light on growth, maturation, and adrenal size of *Microtus montanus*. Amer. J. Physiol. 215:461-466.

Pinter, A.J., and N.G. Negus. 1965. Effects of nutrition and photoperiod on reproductive physiology of *Microtus montanus*. Amer. J. Physiol. 208:633-638.

Pucek, Z. and J. Zejda. 1968. Technique for determining age in the red-backed vole, *Clethrionomys glareolus* Schreber 1780. Small Mamm. News Letter. 2:51-60. Inst. of Ecology. Warsaw.

Reichstein, H. 1964. Untersuchungen zum Korperwachstum und zum Reproduktionspotenzial der Feldmaus, *Microtus arvalis* (Pallus 1779). Z. Wiss. Zool. 170:112-222.

Reiter, R.J., and S.Sorrentino. 1971. Factors influential in determining the gonad-inhibiting activity of the pineal gland. Pages 329-339 *in* G.E.W. Wolstenholme and J. Knight. The pineal gland. Churchill Livingstone, London.

Sadleir, R.M.F.S. 1969. The ecology of reproduction in wild and domestic mammals. Methuen and Co. Ltd., London. 321 pp.

_____ 1974. The ecology of the deer mouse *Peromyscus maniculatus* in a coastal coniferous forest. II. Reproduction. Can. J. Zool. 52:119-131.

Salter, R. 1974. Spring migration of birds in the upper Mackenzie Valley, May 1972. Pages 1-31 *in* W.W.H. Gunn and J. Livingstone. Bird Migration on the North Slope and in the Mackenzie Valley Region 1972. Arctic Gas Biol. Rep. Series Vol. 13. Prepared by L.G.L. Environmental Research Association. Edmonton

Schwarz, S.S., A.V. Pokrovski, V.G. Istchenko, V.G. Olenjev, N.A. Ovtschinnikova, and O.A. Pjastolova. 1964. Biological peculiarities of seasonal generations of rodents, with special reference to the problem of senescence in mammals. Acta Theriol. 8:11-43.

Sealander, J.H. 1966. Seasonal variations in hemoglobin and hematocrit values in the northern red-backed mouse, *Clethrionomys rutilus dawsoni* (Merriam), in interior Alaska. Can. J. Zool. 44:213-224.

Short, R.V. 1972. Role of hormones in sex cycles. Pages 42-72 *in* C.R. Austin and R.V. Short. Reproduction in mammals. Book 3 Hormones in reproduction. University Press. Cambridge. 64 pp.

Sokal, R.S., and F.J. Rohlf. 1969. Biometry. W.H. Freeman, San Francisco. 776 pp.

Stahl, S.S., J.P. Weinmann, I. Schour and A.M. Budy. 1950. The effect of estrogen on the alveolar bone and teeth of mice and rats. Anat. Rec. 107:21-41.

Tupikova, N.V. 1964. Investigations of reproduction and age composition of populations of small mammals. Sect. on reproduction. (Transl. from Russian) Pages 154-170 *in* Methods of investigations of natural foci of human diseases. Publ. House "Medicina", Moscow.

Tupikova, N.V., G.A. Siderova, and E.A. Konovalova. 1968. A method of age determination in *Clethrionomys*. Acta Theriol. 13:99-115.

Talwar, G.P., M.R. Pandian, N. Kumar, S.N.S. Hanjan, R.K. Saxena, R. Krishnaraj, and S.L. Gupta. 1975. Mechanism of action of pituitary growth hormone. Pages 141-170 *in* R.O. Greep Recent Progress in Hormone Research. Proc. 1974 Laurentian Hormone Conference. Vol. 31. Academic Press. New York. 631 pp.

Viitala, J. 1971. Age determination in *Clethrionomys rufocanus* (Sundevall) Ann. Zool. Fennici. 8:63-67.

Viro, P. 1974. Age determination in the bank vole, *Clethrionomys glareolus* Schreb. 1780 from the roots of the teeth. Aquilo Ser. Zool. 15:33-36.

Weitzman, E.D., R.M. Boyar, S. Kapen, and L. Hellman. 1975. The relationship of sleep and sleep stages to neuroendocrine secretion and biological rhythms in man. Pages 399-441 *in* R.O. Greep. Recent Progress in Hormone Research. Proc. 1974 Laurentian Hormone Conference. Vol. 31 Academic Press. New York. 631 pp.

Zejda, J. 1961. Age structure in populations of bank vole, *Clethrionomys glareolus* Schreber, 1780. Zool. Listy. 10:249-264.

Zirul, D.L. 1970. Ecology of the northern red squirrel *Tamiasciurus hudsonicus preblei* (Howell). M.Sc. Thesis. Dept. Zool., Univ. Alta. 131 pp.

Appendix 1 Numbers of Cricetidae present in populations according to snap-trap data. (*C.r = Clethrionomys rutilus, P.m = Peromyscus maniculatus, M.p = Microtus pennsylvanicus, P.i = Phenacomys intermedius*)

Trapping periods	Populations	Number of trap-nights	*C.r*	*P.m*	*M.p*	*P.i*
14-16 VI	Providence Is.	747	5	23	5	0
	Green Island	750	20	14	1	0
17-19 VI	Island 2	552	32	16	0	0
	Island 3	210	5	1	0	0
	Island 1	222	11	2	2	0
20-22 VI	Old Ferry Rd.	1110	11	3	0	0
23-26 VII	Providence Is.	900	29	37	0	1
30-VII-I-VIII	Green Island	898	25	11	0	0
	Old Ferry Rd.	600	4	9	0	0
6-8 VIII	Island 2	645	141	0	3	1
	Island 3	177	15	0	0	0
	Island 1	164*	30	0	1	0
	Long Island	228	17	1	1	0
	Round Island	183	10	16	0	0
9-11 & 13-15 VIII	Simpson Jct.	1189	43	71	0	0
19-21 VIII	Providence Is.	450	57	51	0	0
	Green Island	444*	69	9	0	1
27-29 VIII	Old Ferry Rd.	600	24	15	1	0

*TN adjusted for *Sorex* spp.

Appendix 2 Mean body lengths (mm) and weights (g) of immature males and females in late July and August according to tooth characteristics.

		Length		Weight		Length	Weight
Tooth character	Sex	Mean ± SE	(n)	Mean ± SE	(n)	Significance	
M_1 open	Male	77.47 ± 1.10	(30)	11.09 ± 0.44	(30)	ns	ns
	Female	77.19 ± 1.07	(26)	11.48 ± 0.41	(26)		
M_1 closed	Male	83.46 ± 0.86	(67)	15.59 ± 0.29	(68)	ns	ns
	Female	84.98 ± 0.80	(53)	15.65 ± 0.38	(52)		
M^2 roots 0.1 mm	Male	89.15 ± 0.51	(80)	17.38 ± 0.15	(79)	ns	ns
	Female	89.16 ± 0.83	(50)	17.30 ± 0.21	(50)		
M^2 roots 0.2 mm	Male	90.13 ± 1.34	(15)	17.81 ± 0.49	(15)	ns	ns
	Female	85.20 ± 3.31	(5)	16.22 ± 0.69	(5)		
M^2 roots 0.3 mm	Male	88.13 ± 1.86	(8)	17.50 ± 0.48	(8)		
	Female	- -	(0)	- -	(0)		

Appendix 3 *Peromyscus maniculatus*

In June indices of relative numbers of *P. maniculatus* were highest on Providence Island and Island 2 (Table 5). Only two mature males were trapped on Island 1 and one male was trapped on Island 3. No *P. maniculatus* were trapped on these Islands in August.

Mean litter size based on corpora lutea counts in June was 6.30 (n = 30). Mean litter size based on embryos or new scars in June was 5.70 (n = 30). These values are close to those obtained in the general region by Fuller (1969) for OW animals, but higher than those that Sadleir (1974) calculated for *P. maniculatus* in southern British Columbia (corpora lutea 4.75; embryos 4.52). The differences are in accordance with the general theory of larger litters at higher latitudes. However, since the values in this study were confined to OW animals in June they may be slightly biased. Scar counts were limited to June since sets of scars can be difficult to distinguish in August (Fuller 1969).

In mid June all females were either pregnant and/or had one set of scars, with the exception of one female with two sets of scars. Females on Island 2 (n = 9) showed no evidence of breeding earlier than females on Green Island (n = 9), unlike *C. rutilus* females. No juveniles were trapped in any population in June, which suggests that they were still nestlings, unlike *C. rutilus* which yielded weaned juveniles in all populations except one. All males that were trapped were sexually active.

No attempt was made to age *P. maniculatus* individuals, so the number of young males or females that matured is not known. In late July the testes of all mature males were clearly regressing. Mature

females in late July had, with two exceptions, two sets of scars. None were pregnant. Only four on Providence Island and one at Old Ferry Road were still lactating. In August testes of mature males were still regressing, or had regressed. No females were pregnant and only three females with two clear sets of scars were trapped (one of which was possibly still lactating). However, eight females clearly had one set of scars, the numbers of which ranged from 5 - 8, which was within the range of observed embryos in June. This suggests that those females had matured in the season of their birth. They were divided equally between Providence Island and Simpson Junction. On Round Island, in mid August, only two females had apparently bred, but had scars so faint that no accurate count of a total could be made. Two males that were mature had testes that had regressed to 4 x 2 mm and 3 x 2 mm. Breeding had clearly been terminated for some weeks on this island.

1973 appeared to be an exceptional year in that *P. maniculatus* ceased breeding early in comparison with populations near Heart Lake (50 miles S.E.) in the same year and at least as early as 1967 (Fuller 1969). Cessation was universal, regardless of population numbers. In only three populations, Providence Island, Round Island and Simpson Junction, were *P. maniculatus* present in any numbers in August (indices 13.0, 9.2 and 6.2 respectively). Canham (1969) documented cessation of breeding in a population of *P. maniculatus* in early July, where live-trapping indicated an unusually high density. Sadleir (1974) observed that the breeding season in three populations in different habitats was synchronized over a period of four years. However, there were major differences in times of onset and cessation of breeding between years. No consistent relationship was found with changes in density and changes in breeding.

Dyke (1971) suggested that *P. maniculatus* were dominant over *Clethrionomys* in competition for habitat rather than food. The evidence of this study does not support that suggestion. Virtually the same number of OW females were present on Island 2 and Green Island as *C. rutilus* females in June, yet *P. maniculatus* went to apparent extinction on Island 2 by August and increased from a June index of 1.9 to only 2.4 on Green Island. Simpson Junction and Round Island were not sampled in June and only on Providence Island could an increase in numbers over the summer be documented. What effect this increase might have had on the *C. rutilus* population on Providence Island can only be speculative. It is interesting to note that Canham (1969), while giving no quantitative data, observed that *P. maniculatus* were abundant on Green Island in comparison to *C. rutilus*, while the reverse was observed on Providence Island. The observations are clearly quite different from the situation in the present study. It is apparent that only long-term studies can illuminate inter-specific relationships and extinction and colonization rates on islands.

Population structure and reproductive status of *P. maniculatus*

(P = pregnant, ss = sets of placental scars)

Population	Immature males	Mature males	Immature females	Mature females	P	1ss	P+1ss	2ss
June								
Green Is.	0	5	0	9	1	8	0	0
Providence Is.	0	11	0	12	5	4	3	0
Island 2	0	10	0	9*	0	7	1	1
Island 1	0	2	0	0	-	-	-	-
Island 3	0	1	0	0	-	-	-	-
Old Ferry Rd.	0	3	0	0	-	-	-	-
July								
Green Is.	4	2	3	3	0	1	0	2
Providence Is.	12	5	10	12	0	1	0	11
Old Ferry Rd.	4	0	3	1	0	0	0	1
August								
Green Is.	7	0	1	1	0	1(?)	0	0
Providence Is.	23	2	20	5	0	4	0	1
Island 2	0	0	0	0	-	-	-	-
Island 1	0	0	0	0	-	-	-	-
Island 3	0	0	0	0	-	-	-	-
Round Island	4	2	8	2	0	2(?)	0	0
Long Island	0	0	1	0	0	1(?)	0	0
Old Ferry Rd.	5	2	6	2	0	0	0	2
Simpson Jct.	13	4	17	5	0	4	0	1

*The reproductive tract of an additional female was partially ant-eaten